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THE ST. JOHN'S-WORTS OF CANADA (GUTTIFERAE)

John M. Gillett
Botany Division
National Museum of Natural Sciences
Ottawa, Ontario, Canada K1A 0M8

and

Norman K.B. Robson
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Abstract

This paper is the fourth of a series of family treatments of Canadian plants. In the family Guttiferae, the genus *Hypericum* L. with twelve species (one with two subspecies) and *Triadenum* Raf. with one species containing two subspecies are recognized for Canada. A complete description is given for each species and complete synonyms for all but the weedy species. Typification of accepted names and most synonyms is given where feasible. A key to the species is provided. The classification of *Hypericum* L. by sections is summarized in order to show placement of the Canadian species in the genus. Known chromosome numbers are presented. The weed problem with respect to *H. perforatum* L. is discussed along with several control measures which have been utilized. All species are mapped and illustrated with pencil drawings. Photographs of seeds for each species are provided.

Résumé

Voici le quatrième article d'une série de travaux portant sur les familles des plantes canadiennes. Dans la famille Guttiferae, les genres *Hypericum* L. avec douze espèces (dont l'une contient 2 sous-espèces) et *Triadenum* Raf. avec une espèce contenant deux sous-espèces sont reconnus au Canada. On donne une description complète pour chaque espèce et tous les synonymes à l'exception des mauvaises herbes. Quand cela était possible on a indiqué le type de tous les noms acceptés et de la plupart des synonymes. Une clef pour les espèces est également incluse. La classification par sections de *Hypericum* est fourni afin de démontrer la position des espèces canadiennes. Les nombres des chromosomes connus sont indiqués. On y discute le problème des mauvaises herbes à l'égard de *Hypericum perforatum* L., et plusieurs mesures de contrôle qui ont été utilisées. Toutes les espèces sont cartographiées et illustrées par des graphiques. On y a également ajouté des photographies des graines de toutes les espèces.

Introduction

The family Guttiferae (alternate name: Clusiaceae) has been variously segregated into families or subfamilies. This treatment concerns only the genera *Hypericum* L. and *Triadenum* Raf. because they are the only ones that occur in Canada. Thus it concerns only the subfamily Hypericoideae of Keller's (1893) treatment, a subfamily which was raised to family rank by some recent authors such as Hutchinson (1973) and Takhtajan (1969) but reduced again on rather sound morphological and other grounds by Robson (1977).

Approximately 40 genera and 1,000 species have been placed in the Guttiferae (Willis, 1966) of which many of the genera and species are tropical or subtropical. The genus *Hypericum* L. includes both herbaceous and shrubby members with large numbers of temperate herbs extending north to about 70° N latitude in Europe. The genus *Triadenum* Raf. is also temperate in distribution and includes perhaps 10 species of North America and Asia. The principle revisions of the genus *Hypericum* were by Choisy (1821), Spach (1836), Keller (1893), Keller & Engler (1925) and Kimura (1951). The classification history of the genus has been assembled in chronological sequence by Robson (1977) along with a classification of his own which is a prelude to an eventual monograph of the genus. Some work had been done previously by W.P. Adams (see Bibliography). Recently, the eastern North American species of section *Spachium* were revised (Webb, 1980). *Triadenum* is currently being revised by S.J. Barlow, a student working under the direction of G.J. Anderson of the University of Connecticut, Storrs, Connecticut.

This paper is the fourth in a series of taxonomic treatments of families or genera of Canadian plants by the senior author (Gillett, 1963, 1968; Dunn & Gillett, 1966).

In the interest of relating our native and introduced species to other members of the genus, we are following the classification of Robson (1977). Herbarium abbreviations are according to Stafleu (1978).

Morphology

One of the most interesting features of the Guttiferae is the presence of schizogenous secretory cavities in the leaves (and other organs), which appear as opaque or translucent dots (Metcalfe & Chalk, 1950). These cavities are filled with an oil containing a pigment consisting of an anthocyanin, perhaps a rhamnoside or rhamnosylglucoside of pelargonidin (Siersch, 1927), but no particular use of this substance to the plants has been suggested. Subsequently studies have been made of the distribution of the reddish essential oil hypericin in some 200 species of *Hypericum* by Mathis and Ourisson (1963). They found that practically all hypericin — containing species belong to Keller's sections *Hypericum* and *Campylosporus*.

Another striking feature of the genera discussed here (*Hypericum* and *Triadenum*) is found in the morphology of the seed. All seeds examined (Plates 15-18) are cylindrical with tapered, round or near-round ends and longitudinal rows of foveolae which together give a superficial resemblance to a pill capsule. Extending along the length of the seed, which is nearly straight and tends to roll on a smooth surface, is a variously developed keel. These keels are sticky and easily attach themselves to the dissecting needle. This phenomenon suggests a mechanism for myrmecophily; and, indeed, some species of section *Adenotrias* have caruncles that would seem to be concerned with dispersal by ants.

The classification of *Hypericum* has varied with different authors, as can be seen from the generic synonymy given. The segregation of *Triadenum* as a distinct genus on the basis of several characteristics, including the flesh-colored to mauve-purple or white petals and the presence of large yellow glands alternate with the discrete stamen bundles with largely united filaments, is now generally accepted. However a study of the seeds reveals no significant difference in the seed morphology of *T. virginicum* and any of the *Hypericum* species

studied. The seed of *H. ascyron*, however, differs from the other Canadian species by the broad longitudinal wing and larger overall size. The segregation of *Sarothra* as a separate genus is based solely on the reduction of leaves. Both flower and seed morphology support its retention in *Hypericum*.

Cytology

Chromosome numbers in the species of *Hypericum* were recently summarized by Robson and Adams (1968). These authors considered that there exists a descending series of base numbers of x = 12, 11, 10, 9, 8, 7, of which all but the first and last occur in polyploid forms. Most of the species of *Hypericum* counted are either diploid or tetraploid. However *H. perforatum* is diploid and tetraploid based on a count made on material of European origin by Noack (1939), and hexaploid based on a count by Robson (*in litt.*). Counts on American material of this widely distributed weed made by Hoar and Haertl (1932), by Mulligan (1957) and by Adams (in Robson & Adams 1968), indicate the existence of diploid and tetraploid levels only. Both pentaploid and hexaploid levels have been found in the hybrid *H.* x *desetangsii* Lamotte (= *H. perforatum* x *maculatum* Crantz) by Robson (1956) and reported in Robson and Adams (1968). With respect to *H. perforatum* also, Noack (1939) showed that the tetraploid phase of this species is apomictic. Most embryo sacs produce seed without pollination being necessary. Rings of 16 chromosomes have been observed by Adams (in Robson and Adams, 1968) and Hoar (1931) in *H. mitchellianum* and in *H. punctatum* respectively, two closely related species. This phenomenon, which parallels the situation in *Oenothera*, and its accompanying meiotic irregularities are probably responsible for variation in haploid number and in the abortion of pollen grains.

The species *Triadenum virginicum* (L.) Raf. was counted by Hoar and Haertl (1932) and an *n* number of 19 was obtained. This genus was recognized as distinct by Robson and Adams (1968). The chromosome number lends support to the several morphological characteristics which distinguish this genus from *Hypericum*.

Taxonomy

Guttiferae

Trees, shrubs or herbs with resinous sap. Leaves opposite, alternate or whorled, simple, pellucid or black punctate, usually exstipulate occasionally stipulate (*Garcinia*). Flowers bisexual (subfamily Hypericoideae) or unisexual and polygamomonoecious, actinomorphic, cymose. Perianth biseriate, sepals 4-5 (subfamily Hypericoideae) or 2-10, often basally connate, the outer ones smaller than the inner. Petals as many as the sepals or twice as many, often oblique, distinct (or similar in *Calophyllum*), imbricate or contorted, convolute in the bud. Stamens numerous, seldom less than 10, in 5(4) antipetalous fascicles, often obscured by fusion or merging, often alternating with 5 sterile antisepalous fascicles or, if only 3, then one of these antisepalous, anthers 2-celled, longitudinally dehiscent. Ovary superior, (1) 3-5(-12) carpellate and -loculed, more rarely unilocular, placentation axile to parietal, ovules usually numerous, styles (1) 2-5 distinct or more or less connate or absent. Fruit a septicidal (rarely septicidal and loculicidal) capsule, berry or drupe. Seed without endosperm.

Hypericum L. Sp. Pl. 2: 783. 1753
as *Hypericon*, orth. mut. J.F. Gmelin, Syst. Nat. 2: 1156. 1791.
Sarothra L. Sp. Pl. 1: 272. 1753. Type: *S. gentianoides* L.

Type genus: *Clusia* L. Type genus of the frequently segregated family Hypericaceae: *Hypericum* L.

Key to the genera:

A. Petals yellow or orange, convolute in the bud, stamens mostly numerous, distinct or united merely at the base into 3-5 clusters, without intervening sterile stamen fascicles (fasciclodes) ..... **Hypericum** L.

AA. Petals flesh-colored to mauve-purple, imbricated in the bud, stamens mostly 9, strongly triadelphous, with 3 large orange fasciclodes alternating with the stamen bundles ..... **Triadenum** Raf.

Table 1. — Chromosome numbers of Canadian native and introduced species of Guttiferae

Species	*n*	*2n*	
Hypericum anagalloides C. & S.		16	Gillett 15511, between 1st & 2nd Nanaimo Lakes, Vancouver Island, B.C. June 21, 1970
H. canadense L.	8		Hoar & Haertl, 1932
		16	Webb & Halliday, 1973
H. ellipticum Hooker	9		Hoar & Haertl, 1932
		c18	Gillett, 1975
H. gentianoides (L.) B.S.P.	12		Hoar & Haertl, 1932
H. kalmianum L.		18	Hoar & Haertl, 1932
H. majus (Gray) Britt.	8		Hoar & Haertl, 1932
H. mutilum L.	8		Bell, 1965
ssp. *boreale (Britt.)* J.M. Gillett	8		Hoar & Haertl, 1932
(as *H. boreale* (Britt.) Bickn.)			
(as *H. boreale*)		18	Kapoor, 1972
H. perforatum L.	16, 17, 18		Nielsen, 1924
	16		Winge, 1925
	16		Hoar & Haertl, 1932
	16	32, 48	Noack, 1939
		32	Mulligan, 1957
		32	Hedberg & Hedberg, 1964
		32	Gadella & Kliphuis, 1967
		32	Nilsson & Lassen, 1971
		32	Holub *et al.*, 1972
		32	Reynaud, 1973; Loeve & Kjellqvist, 1974
H. prolificum L.	9		Nielsen, 1924
	9		Adams *in* Robson & Adams, 1968
H. punctatum Lam.	8 (ring of 16)		Hoar, 1931
	7		Bell, 1965
	8 (ring of 16)		Adams *in* Robson & Adams, 1968
H. scouleri Hook. (as *H. formosum* HBK ssp. *scouleri* (Hook.) C.L. Hitchc.	8		Kyhos, 1967
Triadenum virginicum (L.) Raf. ssp. *fraseri* (Spach) J.M. Gillett	19	38	Hoar & Haertl, 1932
	19		Mosquin (unpublished from herbarium specimen vouchers, DAO)

Knifa Adans. Fam. Pl. 2: 444, 541, 1763. Lectotype: *H. mutilum* L.

Roscyna Spach, Hist. Nat. Vég., Phan. 5: 426. 1836. Type: *R. gmelinii* Spach = *H. ascyron* L.

Brathydium Spach, l.c. 5: 442. 1836. Lectotype: *B. dolabriforme* (Vent.) Y. Kimura.

Myriandra Spach, l.c. 5: 434. 1836. Type: *M. prolifica* (L.) Spach.

(Only generic names including Canadian species are given. For more complete synonymy see Robson (1977).)

Herbs or deciduous-leaved shrubs with opposite, punctate, black-dotted, striiform or linear glandular leaves, or the leaves reduced to scales. Flowers yellow, in terminal cymes or also axillary, rarely solitary. Sepals 4 or 5, equal or unequal. Petals 4 or 5, oblique or somewhat contorted, convolute in the bud. Stamens 5-many, free or united below or united into discrete bundles, these without large hypogynous sterile stamen fascicles between them, except in sections *Adenotrias* and *Elodes*. Filaments slender, elongate, anthers longitudinally dehiscent. Ovary 2-5 — carpellate, 1-celled or partially divided by the intrusion of the parietal placentae, or completed 3-5-celled. Styles free or more or less connate, often later separating, persistent on the valves of the fruit. Capsule globose, ovoid or conic, usually septicidally dehiscent apically. Seeds numerous, elongate, usually with rounded ends, longitudinally papillose or reticulate, often with an elongate wing.

Type species: *H. perforatum* L.

Key to the sections:

A. Petals and stamens, or only petals, deciduous after anthesis ..... **Myrianda**

AA. Petals and stamens persistent after anthesis

B. Stamens in a continuous narrow ring ..... **Spachium**

BB. Stamens in fascicles or irregularly arranged

C. Styles appressed or more or less united, mostly 5, sometimes 4; stamen fascicles 5 or 4 ..... **Roscyna**

CC. Styles free, spreading or ascending, not appressed, mostly 3; stamen fascicles 3, rarely 4 or 5 ..... **Hypericum**

Section **Myrianda** (Spach) R. Keller

Key to the species:

A. Ovary unilocular; herbs with usually elliptic leaves ..... **H. ellipticum**

AA. Ovary appearing 3-5-locular by intruding parietal placentae; small woody shrubs

B. Flowers in terminal open cymes or corymbs or solitary; capsule of usually 5 carpels; leaves linear-elliptic, acute ..... **H. kalmianum**

BB. Flowers in terminal contracted corymbs and also in the axils below, capsule of usually 3 carpels; leaves oblanceolate-elliptic, obtuse or rounded ..... **H. prolificum**

Hypericum ellipticum Hook., Fl. Bor. Am. 1: 110. 1830.

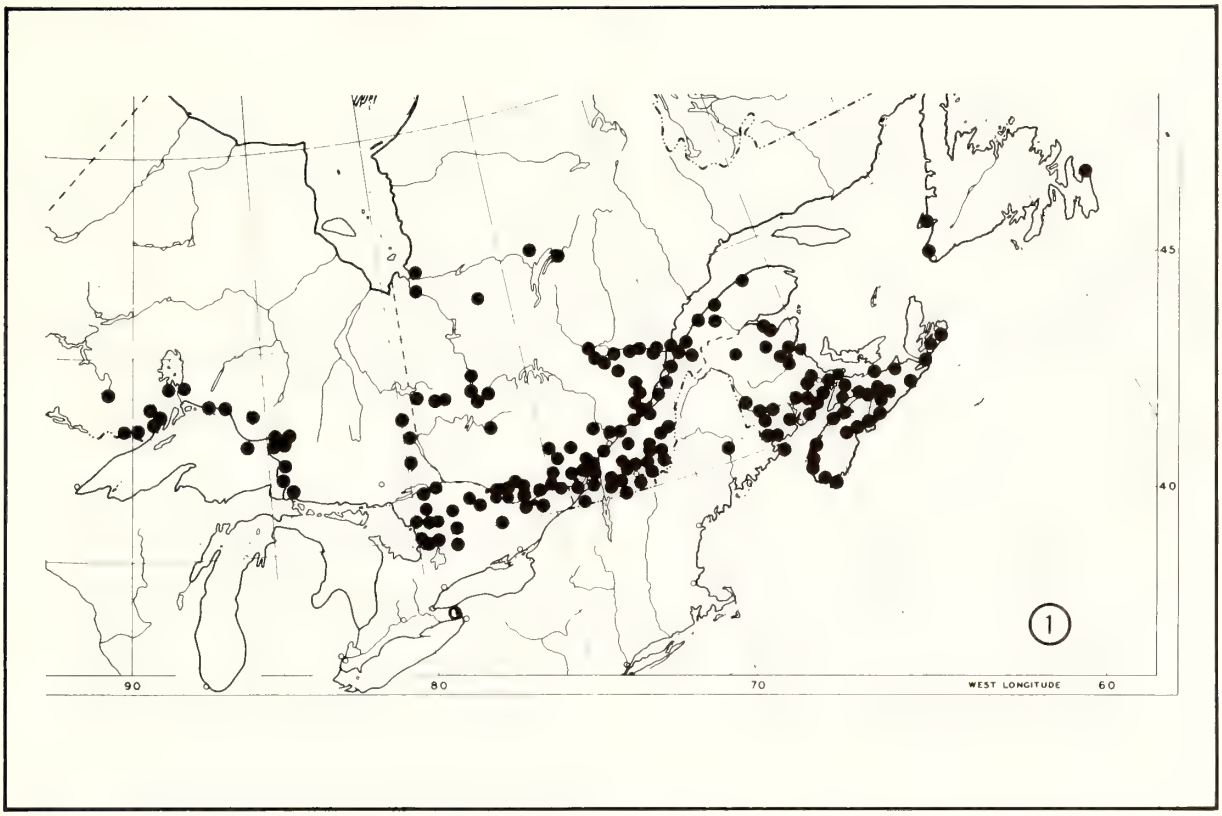
Brathydium canadense Spach, Hist. Nat. Vég., Phan 5.442. 1836, et Ann. Sci. Nat. sér. 2. 5: 365. 1836.

H. ellipticum f. *submersum* Fassett in Rhodora 41: 376. 1937. Type: Ontario, Pipe Lake, Jack Wilson's Resort, Walford, 5 August 1936, *Fassett 19172*, Holotype WIS.

H. ellipticum f. *foliosum* Marie-Victorin in Nat. Canad. 71: 201. 1944. Type: Québec, comté de Portneuf, Rivière du Cap Rouge. 7 septembre 1941. *Victorin, Rolland, Kucyniak, & Raymond 56602* MT.

Common Name: Pale St. John's-wort. Plates 1, 15, Map 1.

Herbaceous, glabrous rhizomatous perennials, 1.1-(2.2)-3.0 cm tall, somewhat woody at the curved ascending base, the stem simple, occasionally branched below or with axillary fascicles (often due to damage to the stem apical meristem and subsequent stimulation of lateral buds), indistinctly



Map 1. Distribution of *Hypericum ellipticum* Hook.

2-ridged and angled, often somewhat flattened, not persisting to the following season. Roots fibrous, arising from the base of the stem or from the rhizome nodes. Leaves pellucid, sessile, clasping or nearly so, the pairs spirally arranged but not decussate, elliptic, obovate, linear-elliptic to oblanceolate, those of the fascicular branches smaller and more slender than the principal cauline leaves, the median leaves 1.1-(2.2)-3.1 cm long, 0.3-(0.8)-1.3 cm wide, the lower progressively smaller, closer spaced, withering and eventually caducous. Flowers solitary or in simple or corymbiform cymes, at least the terminal one showy, ca. 1.3 cm in diameter, yellow, occasionally suffused with pink. Sepals 5, slightly united at the base, oblanceolate, one pair usually larger than the others, ca. 7 mm long, 2 mm wide, acute with a thick midvein with 2 smaller lateral veins from the base, reticulate venation between them. Petals obovate, the largest 8 mm long, 3.5 mm wide, the shortest 6 mm long, nearly 4 mm wide. Stamens very numerous, yellow, the anthers ca. 0.5 mm in diameter and long. Pistil 0.3—0.4 cm long, sessile, ovoid, the carpels indistinct, locule 1, with 3 intruding parietal placentae, the styles 3, often fused or late separating, about the same length as the ovary but slightly longer than the stamens, the stigmas terminal. Capsule deep maroon, ellipsoid, 4-7 mm long, with persistent stamens turning maroon, the slender styles separating to the base or not at all. Seeds cylindrical with rounded ends and a longitudinal wing along one side, the surface pitted, ca. 0.5 mm long.

Pale St. John's-wort occupies wet habitats such as swamps, stream and lake margins, beaver ponds and meadows. Flowering takes place from June to August with the peak in late July; fruiting begins in mid-August and continues to mid-September.

This species is distinctive by its long styles separating slightly in fruit, the deep maroon capsule and the usually elliptic leaves. Often it forms extensive stands along wet beaches or at the water's edge along streams or lakes.

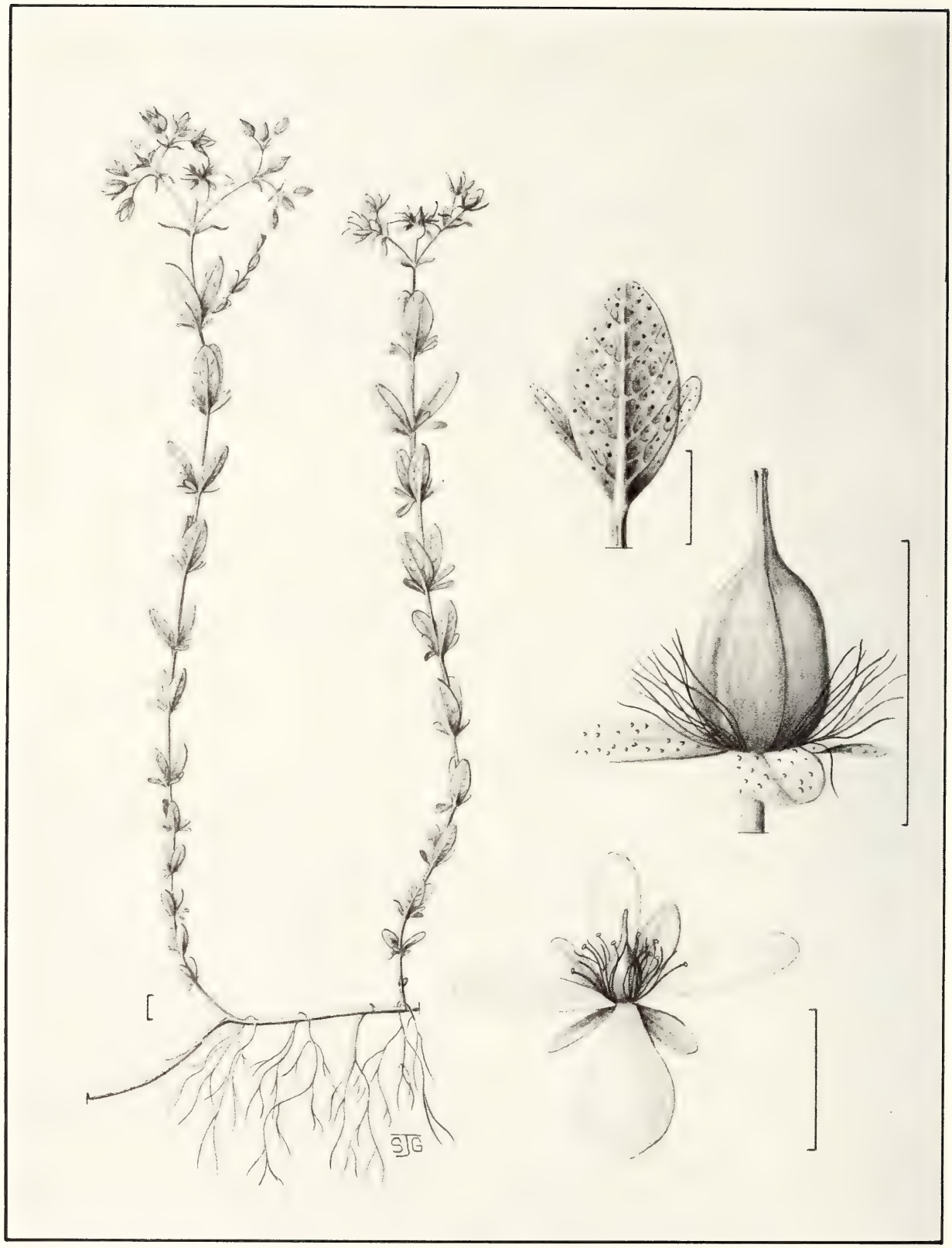


Plate 1. *Hypericum ellipticum* Hook.
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

Hypericum kalmianum L., Sp. Pl. 2: 783. 1753. Type: Virginia, Kalm, LINN 943.2.

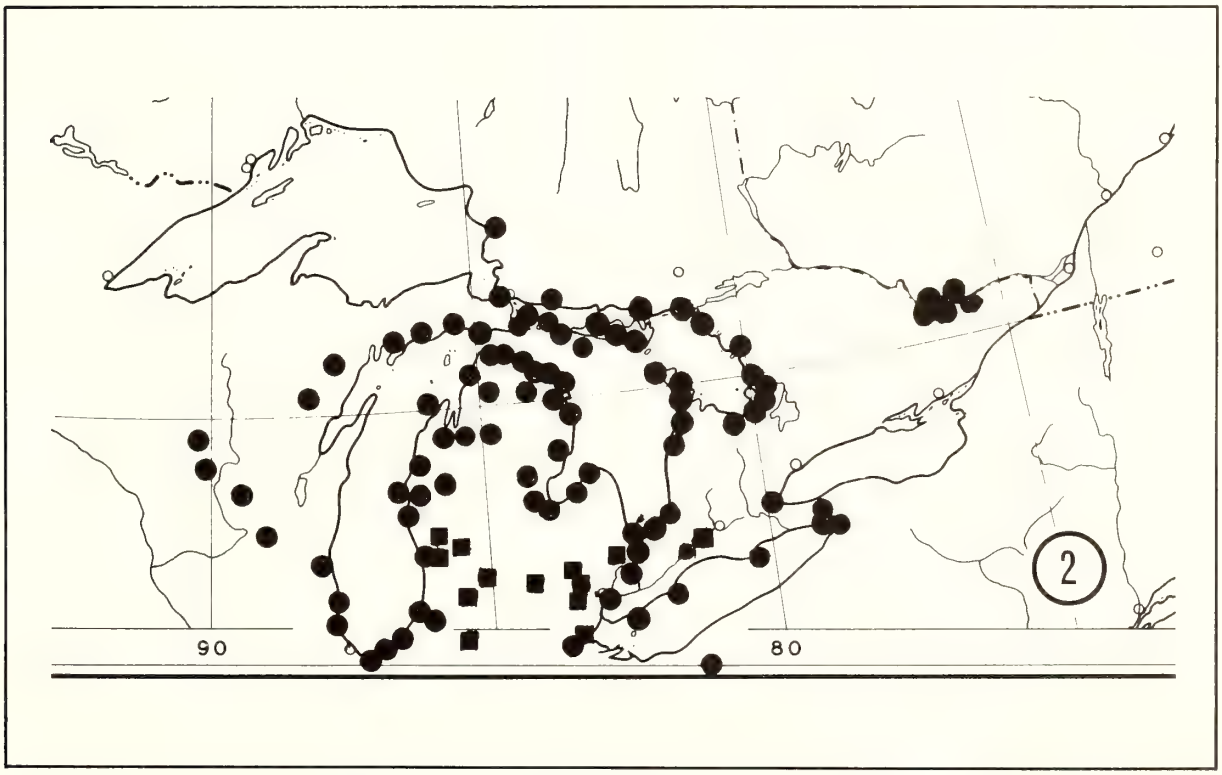
Norysca kalmiana (L.) K. Koch, Hort. Dendrol. 66. No. 6, 1853.

Common Name: Kalm's St. John's-wort. Plates 2, 18. Map 2.

Small shrub 2.5-6.0 dm tall with reddish-brown stems, papery grayish bark and ascending branches. Branches 4-angled, the twigs appearing 2-angled, almost winged, by suppression of two angles. Leaves crowded, sessile or very short-stalked, linear, linear-oblong to oblanceolate, 1.5-4.0 cm long, 3-7 mm wide, obtuse, pale below, glabrous with pellucid dots, dark green to reddish above, occasionally with clusters of small leaves in the axils, the midvein prominent below, channelled above, the margins revolute. Inflorescence a simple cyme, or a terminal 7-flowered dichasium, or the flower solitary, the lateral stout pedicels longer than the terminal. Flowers yellow, showy, the sepals thickened, soon divergent or reflexed, oblong to obovate, 5 or 4, then one pair slightly larger than the other, 6 mm long, 3.5 mm wide, obtuse, punctate, the petals asymmetrical, oblong to obovate, rounded, 1.5 cm long, 0.7 cm wide. Stamens slender, very numerous, 150-200, free, occasionally a few united, the anthers 0.25 mm long, rounded. Receptacle 0.5 mm thick. Ovary 0.8 cm long, slender ovoid, deep plum to purple, the styles 3-(5)-6, 0.3 cm long, united below. Capsule deep purple, 1.1 cm long, 0.4 cm wide, the styles persisting as a beak, locules as many as the styles. Seeds 1 mm long, purple, beaked at each end.

Sandy shores and dunes, limestone and calcareous shores of lakes and rivers. Flowering from early July to about mid-August; fruiting from early August until early October.

Adams (1962) was of the opinion that the closest relative of *H. kalmianum* was *H. lobocarpum* Gattinger (= *H. oklahomense* Palmer), which in turn closely approaches *H. densiflorum* Pursh of the Appalachians. However upon examination of the morphology of these species and a perusal of the distribution maps published by Utech & Iltis (1970) which were based on some unpublished Adams maps, we have the impression that the closest relative to *H. kalmianum* is *H. prolificum* and that *H. lobocarpum* relates to *H. densiflorum* Pursh. The entire range of *H. kalmianum* is in what we consider to be glaciated territory and *H. prolificum* extends from south of the line of



Map 2. Distribution of *Hypericum kalmianum* L. — solid dots and of *H. prolificum* L. —solid squares

Plate 2. *Hypericum kalmianum* L.
Habit; flower; fruit with 3 styles; fruit with 5 styles; portion of stem. Measurements in centimeters unless otherwise indicated

maximum extent of glaciation into the area of *H. kalmianum*. Geographical distribution is a powerful indicator of relationships between populations and may indicate the proper emphasis to be given to certain morphological characteristics. In this case the suspect ones are carpel number and degree of lobulation of carpels, which obviously vary in the group.

Kalm's St. John's-wort has a curious distribution. It was mapped by Soper and Heimburger (1961) for Ontario and for Michigan by Guire and Voss (1963). The latter authors admitted that some inland locations were beyond the range of their map. The most significant omission was from along the Ottawa River above Ottawa (placed rather vaguely by Utech & Iltis 1970). Here *H. kalmianum* is found at Shirley Bay just west of Ottawa, then appears along Lac des Chats at Bristol, Sand Bay and on Morris Island west of Quyon, where it occupies limestone shores. Guire and Voss (1963) suggested that the type came from near Niagara, where Kalm visited during his journey; Linnaeus gave "Kalm, Virginia" but it is not found in present-day Virginia.

Gattinger (1887) described a variety *majus* for this species which he said was 5-7 ft high. Undoubtedly this was confused with some other species or perhaps genus.

Hypericum prolificum L., Mant. 1: 106. 1798. Lectotype LINN 943.20 selected by Svenson in Rhodora 42: 9. 1940.

Myriandra spathulata Spach, Hist. Nat. Vég., Phan. 5: 440. 1836. Type: *Leconte*, P.

M. prolificum (L.) Spach, l.c.

H. spathulatum (Spach) Steud., Nomencl. ed. 2. 1: 789. 1840, not R. Keller in Engler, Bot. Jahrb. 58: 195. 1923, hom.

Common Name: Shrubby St. John's-wort. Plates 3, 18. Map 2.

Erect shrub 0.2-2 m tall with erect or ascending 4-angled branches, shreddy gray bark and 2-edged branchlets. Leaves elliptic to oblong or oblanceolate, 3-7 cm long, 0.8-1.5 cm wide, flat to revolute margined, sessile or with short petioles (to 3 mm long), tapering to the cuneate base, the apex rounded or obtuse, often retuse or mucronate, pale below with scattered punctae, the midvein prominent and with obscure lateral reticulations. Clusters of smaller linear-oblong to linear-oblanceolate petiolate leaves 1.0-2.5 cm long in the axils. Cymes compound, 10-20-flowered, terminal and axillary in the upper 2-3 axils and borne on thickened peduncles. Flowers yellow, 1.0-2.0 cm in diameter. Sepals somewhat thickened, unequal, shorter than the petals, ovate, mucronate, 0.3-6.0 mm long, 2.0-2.5 mm wide. Petals asymmetrical, obovate, 4.5-14 mm long, 4.0-4.5 mm wide, rounded. Stamens slender, numerous, free, anthers 1 mm long. Ovary unilocular, appearing 3(4-5) locular by 3(4-5) intruding parietal placentae. Styles 3 sometimes 4 or 5, united below, 2.5-3 mm long. Capsule ovoid, 6-13 mm long, the styles persisting as a beak, often broken off. Seeds purple, ca. 1-1.4 mm long, cylindrical, straight or curved, beaked at the ends, longitudinally striate.

The shrubby St. John's-wort is mainly a woodland species but may be found on limestone ledges, sandy places, river bottoms and gorges. Flowering takes place from the second week of July to early August when fruits begin to appear, remaining until about mid-September.

The application of the name *Hypericum prolificum* L. has occasioned a certain amount of difficulty. Svenson (1940), in a study of the woody species of *Hypericum* of the eastern United States, examined the Linnaean herbarium material and stated that there were 5 sheets, Nos. 20-24 incl. (now 943.20-943.24 of Savage's Catalogue), in the Linnaean herbarium. He selected No. 20 as lectotype of *H. prolificum* L., remarking that the sheet represented an aberrent specimen of *H. prolificum* in the accepted sense. Then Fernald and Schubert (1948), while concurring with Svenson's choice, were not satisfied that it was truly *H. prolificum* as accepted and that it was specifically distinct from the other four sheets. Svenson (1952) defended his selection and his identity of the material on the grounds that the revolute leaves on the Linnaean sheet represented merely an ecological varient of the others. Subsequently, Adams (1959) supported Svenson's use of *H. prolificum*, stating that all five sheets of the Linnaean material represented the plant known as *H. prolificum* L. and that *H. spathulatum* (Spach) Steud., taken up by Fernald and Schubert, should be relegated to synonymy.

Plate 3. *Hypericum prolificum* L.
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

Key to the species:

A. Leaves all scale-like, subulate or linear-subulate, 0.5-2.5 mm long; stems fastigiately branched; capsules very narrowly ovoid, conspicuously exceeding the calyx ..... **H. gentianoides**

AA. Leaves, linear, ovate or elliptic to oblanceolate, not reduced

B. Capsule ellipsoid, the summit rounded; sepals oblong to elliptic

C. Capsule about as long as the elliptic sepals; leaves elliptic, crowded; mat or clump-forming species with few branches ..... **H. anagalloides**

CC. Capsule longer than the oblong sepals; leaves ovate or elliptic, separated; plants solitary and usually branched above ..... **H. mutilum**

BB. Capsule conic or ovid, the summit tapered; sepals lanceolate

D. Leaves and sepals lanceolate; leaf veins 3-5 at the base; sepals attenuate, 4-7 mm long; capsule ovoid, 0.5-0.6 mm long ..... **H. majus**

DD. Leaves linear-oblanceolate; leaf veins 1-3; sepals acute to blunt, 2.5-4.5 mm long; capsule conic, 0.4-0.5 mm long ..... **H. canadensis**

Hypericum gentianoides (L.) B.S.P., Prelim. Cat. N.Y. Pl. 9. 1888.

Sarothra gentianoides L., Sp. Pl. 1: 272. 1753. Type: *Clayton 110* BM!

H. nudicaule Walt., Fl. Carol. 190. 1788. Type: Carolina, *Walter* f. 60, No. 649 BM!

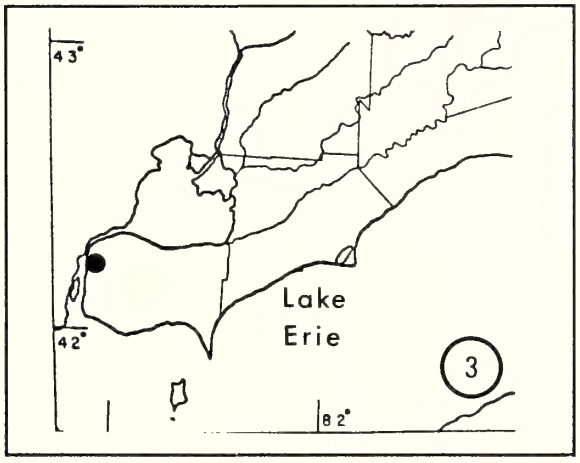
H. sarothra Michx., Fl. Bor. Am. 2: 79. 1803. Nom. illegit.

S. hypericoides Nutt., Gen. Pl. 1: 204. 1818, new name for *S. gentianoides* L.

Brathys gentianoides (L.) Spach, Hist. Nat. Vég., Phan. 5: 440. 1836.

Common Names: Orange-grass; Pineweed. Plates 4, 16. Map 3.

Simple or fastigiately branched annuals, the branches few to copious, arising from the upper two-thirds of the plant, occasionally from the base, the lower branches usually opposite, the upper alternate; stems and branches wiry, gland-dotted, sometimes purpled, four-angled and winged, squarish in cross-section or sometimes flattened. Leaves 0.5-2.5 mm long, scale-like, subulate, opposite, with a single row of glandular dots, very slightly carinate, the keel continuous with the narrow stem wing, the first two pairs of leaves ovate to rounded. Flowers solitary or in pairs, rarely in simple axillary or terminal cymes, sessile or nearly so. Sepals 5, equal, 2.0 mm long, 0.5 mm wide, lanceolate-subulate, with a longitudinal streak on each side of the single midvein. Petals 5, about the same length as the sepals, orange-yellow to yellow, oblong, 3-5-veined, the tips tending to twist after anthesis. Stamens 5 to 10, free. Pistil yellow, about the same length as the petals and sepals, styles 3, separate and spreading. Capsule 6-7 mm long, lanceolate, profusely streaked, the 3 valves separating half the length of the capsule. Seeds oblong-cylindrical with rounded ends, longitudinally striate, 0.75 mm long, yellowish.



Map 3. Distribution of *Hypericum gentianoides* (L.) B.S.P.

Hypericum gentianoides is found in a variety of habitats such as sandy places, in damp pockets of soil in rocky places, along stream banks, along railway tracks, roadsides, wet ditches, fields and moist swampy areas.

Flowers and fruit are often found together on the same plant, but for the most part flowering takes place from mid-June to early September. Fruits appear in greatest density from late August to November and irregularly at an earlier date depending on conditions.

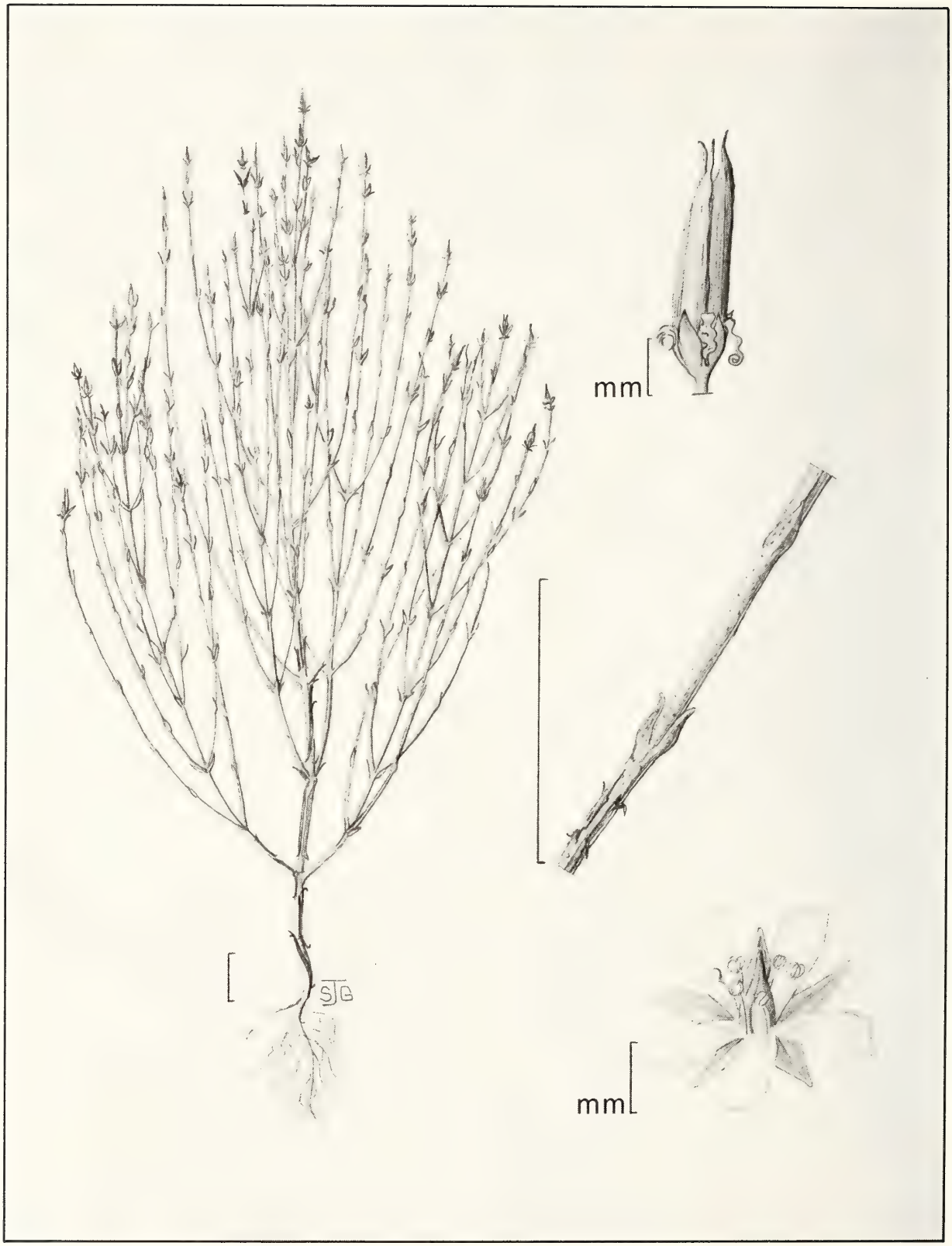


Plate 4. *Hypericum gentianoides* (L.) B.S.P.
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

This species is obviously closely related to *H. drummondii* (Grev. & Hook.) Torrey & Gray, which does not get as far north as Canada. These plants have been placed in a separate genus *Sarothra* L. by various authors since Linnaeus's time but the characteristics distinguishing them do not warrant their segregation. Britton & Brown (1897) rather inconsistently placed *H. gentianoides* in *Sarothra* and *H. drummondii* in *Hypericum*.

From Map 5 it is evident that *H. gentianoides* species is an endangered species in Canada, being confined to a very small area of the Windsor prairie. Fortunately, steps have now been taken to protect this interesting area, which contains a number of other species in danger of extinction by urban and industrial expansion.

Hypericum anagalloides Cham. & Schl. in Linnaea 3: 127. 1828.

Type: California, San Francisco, *Chamisso* LE.

Hypericum anagalloides var. *nevadense* Greene, Fl. Fran. 113. 1891. Type: California, near Calistoga, June 19, 1874, *Greene 231* MO.

H. bryophytum Elmer in Bot. Gaz. 36: 60. 1903. Type: Washington, Clallum County, Olympic Mountains, August 1900, *Elmer 2833* DS.

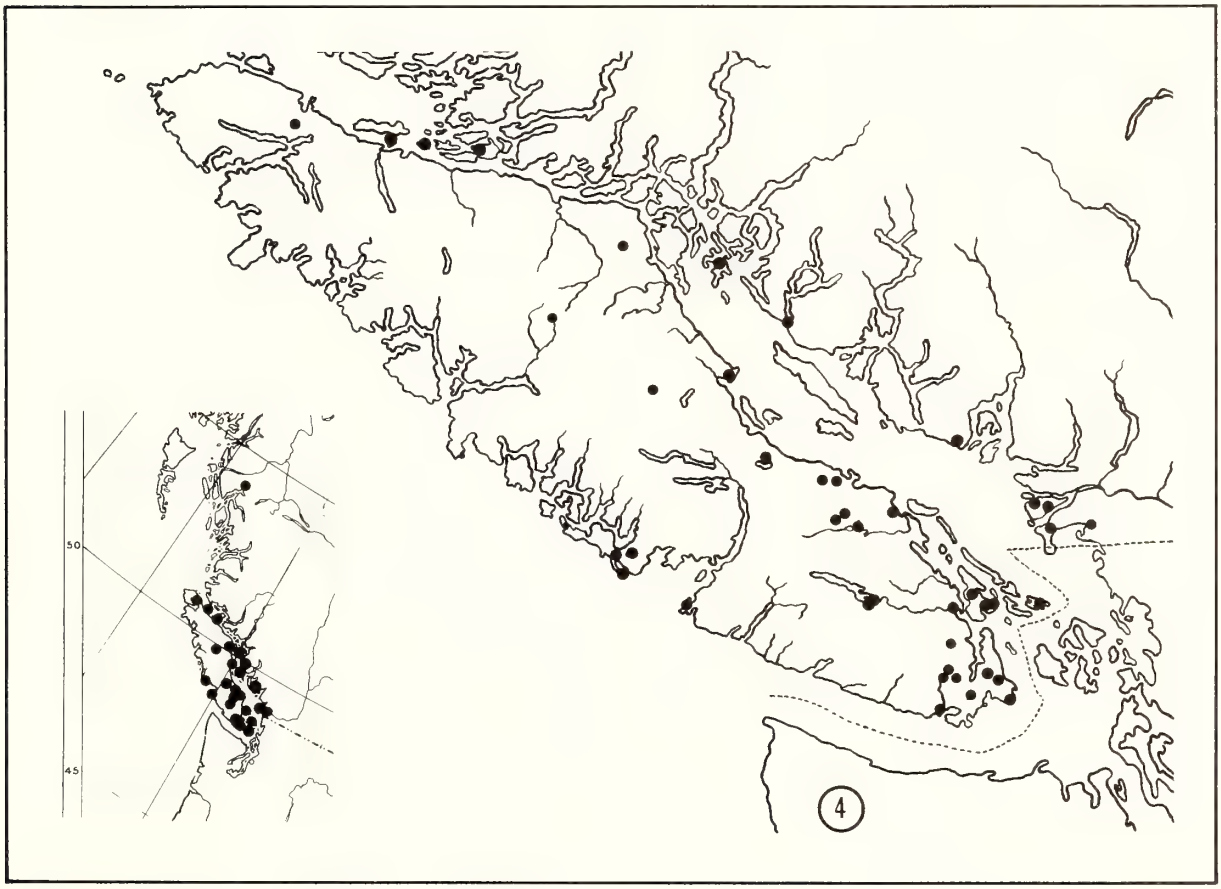
H. anagalloides var. *calicifolium* R. Keller in Bull. Herb. Boiss., sér. 2, 8: 187. 1908. Type: California.

H. anagalloides var. *cymosum* R. Keller in Bull. Herb. Boiss., sér. 2, 8: 187. 1908. Type: California, Santa Cruz, June 4, 1887, *Jones* BM,BR,P.

H. anagalloides var. *pumilum* R. Keller in Bull. Herb. Boiss., sér. 2, 8: 187. 1908. Lectotype: Oregon, Cascade Mts., 1859, *Lyall 346* W, isolectotype K,P.

H. anagalloides var. *ramigerum* R. Keller in Bull. Herb. Boiss., sér. 2, 8: 187. 1908. Lectotype: California, San Bernardino Mts., August 1884, *Parish & Parish 623* BR, isolectotype, US.

H. anagalloides var. *undulatum* R. Keller in Bull. Herb. Boiss., sér. 2, 8: 186. 1908. Type: California, *Kellogg & Hartford 104* P, US.



Map 4. Distribution of *Hypericum anagalloides* C. & S.

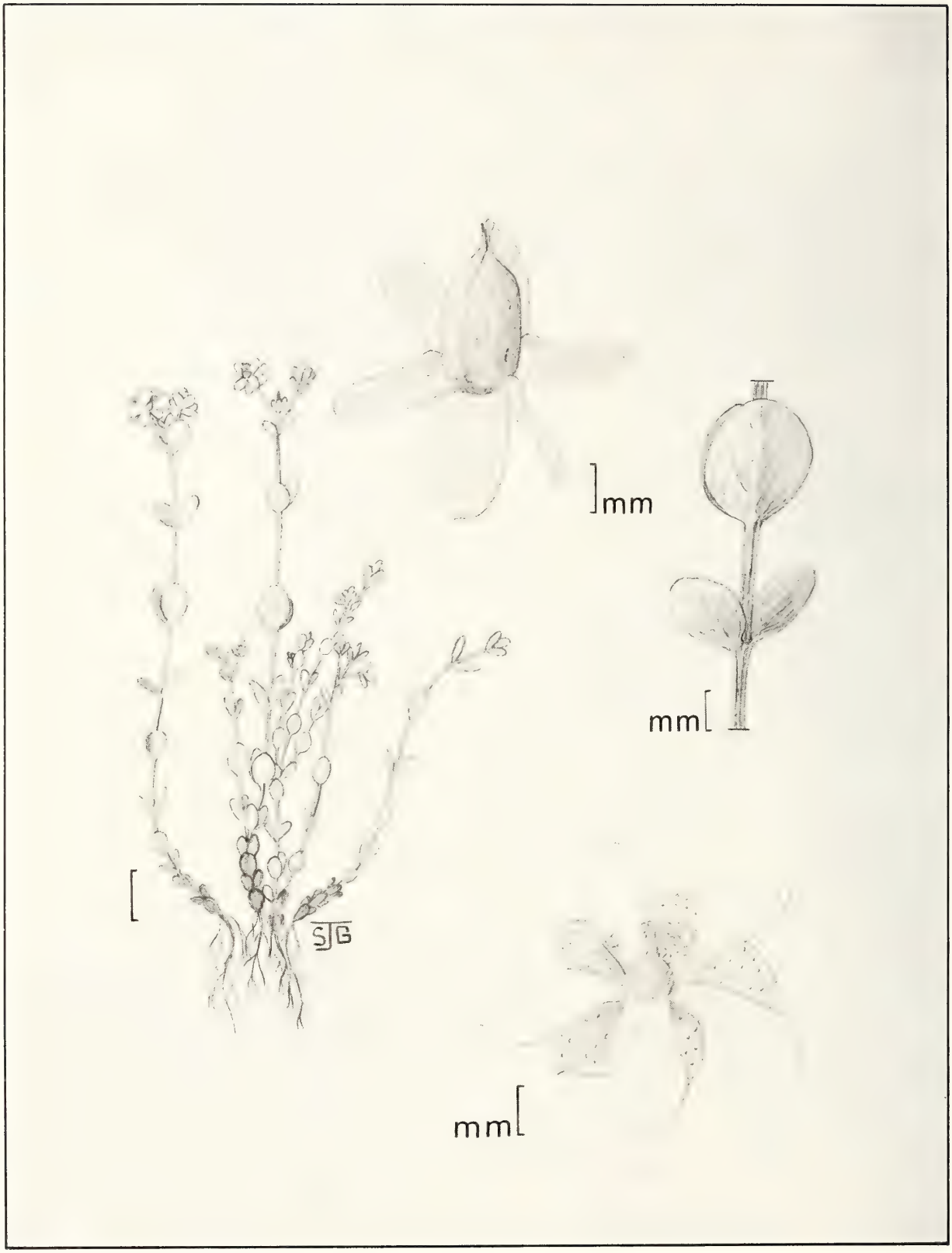
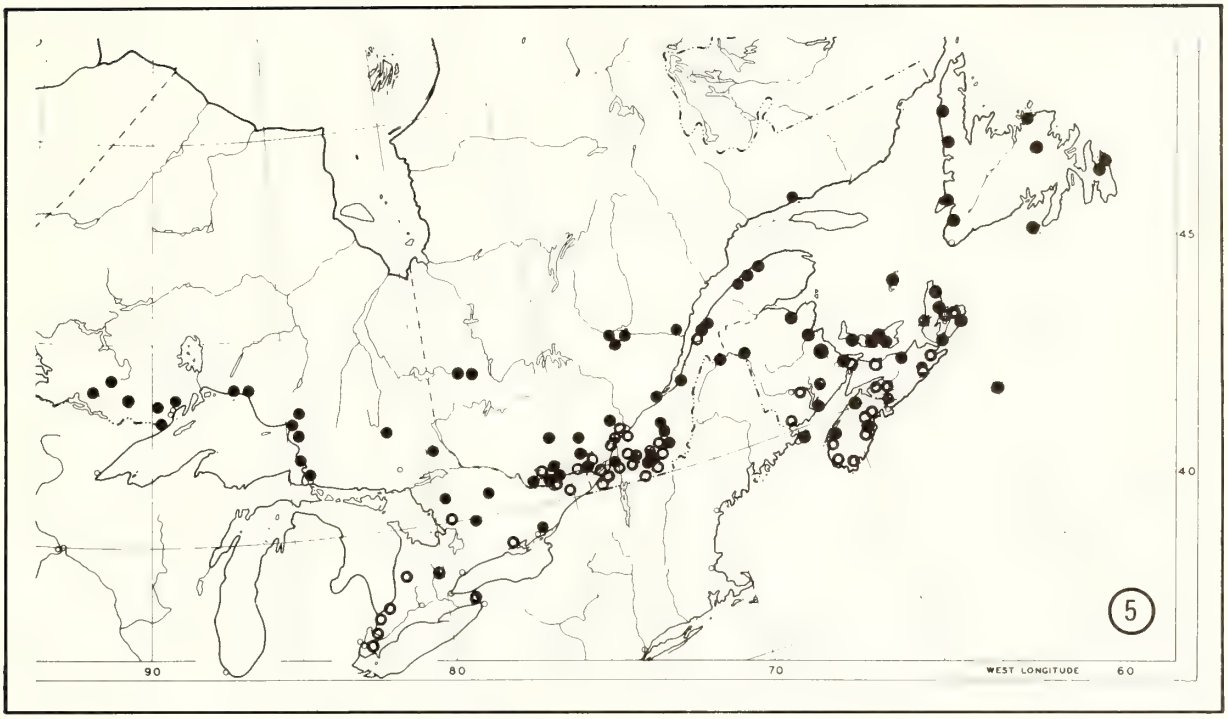


Plate 5. *Hypericum anagalloides* C. & S.
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated



Map 5. Distribution of *Hypericum mutilum* L.
ssp. *mutilum* — open circles
ssp. *boreale* (Britton) J.M. Gillett — solid dots; intermediates — half circles

H. tapetoides A. Nels. in Bot. Gaz. 52: 266. 1911. Type: Idaho, Silver City, July 22, 1910. *Macbride 453*.

Common Names: Creeping St. John's-wort, Tinker's Penny. Plates 5, 15. Map 4.

Diffuse, mat-forming perennials, 0.3-1.5 dm tall, the stems curved-ascending at the base or strict, the internodes very short, progressively shorter towards the base and bearing reduced leaves, the stems slender, slightly flattened to squarish with narrow wings, simple or branched above. Roots fibrous, in dense masses arising chiefly from the vertical or horizontal rhizome. Upper cauline leaves ovate, elliptic to obovate, 0.5-(0.7)-1.0 cm long, 0.3-(4.0)-0.6 cm wide, the apex obtuse to rounded, somewhat clasping at the base, the lower leaves progressively smaller and more crowded, tending to be obovate with tapered base, midveins of the upper leaves more prominent than the 2-3 laterals, the punctae not prominent, rather evenly spaced. Flowers solitary and terminal or in simple or compound cymes closely subtended by leaf-like or reduced bracts.* Sepals 4-5, ovate-elliptic to oblong, rounded or apiculate, unequal, the larger 2-3 mm long, 1.5-2.0 mm wide, sometimes united at the base, streaked with oil glands. Petals yellow to salmon-coloured, obovate, rounded, only slightly longer than the sepals, strongly veined. Stamens 15-20, about equal to the sepals or shorter but longer than the ovary and styles, anthers round, ca. 0.25 mm in diameter, the thecae yellow. Ovary 2 mm long, ovoid, the 3 styles 1.5 mm long, strongly divergent, stigmas capitate. Capsule 3 mm long, oblongoid, concealed by the sepals for the most part.

Creeping St. John's-wort grows in wet places such as ditches, banks of streams, edges of lakes and meadows. It is also found in bogs. Flowering takes place almost throughout the growing season from May to September. In Canada it occurs on Vancouver Island and on the mainland near Vancouver, but tne total range extends to Baja California.

This species has been cultivated in the greenhouse from material collected from Nanaimo Lakes, B.C. and a chromosome count was obtained. In the field it grew along grassy banks of a stream in company with *H. scouleri* ssp. *scouleri*. It is an extremely attractive plant, producing tufts which bear large numbers of tiny flowers.

*Bracts of the inflorescence of plants from the southern part of the range in California and Nevada are nearly always reduced or subulate. "Reduced" bracts are considered to be the primitive condition.

Hypericum mutilum L., Sp. Pl. 2: 787. 1753. Type: *Clayton 232* BM!

H. quinquenervium Walt., Fl. Car. 190. 1788. Type: Carolina, Walter f. 60. No. 692 BM!.

H. stellarioides H.B.K., Nov. Gen. Pl. 5: 196. Type: Colombia, in monte Quindiu, *Humboldt & Bonpland* P!

Brathys quinquenervia (Walt.) Spach, Ann. Sci. Nat., sér. 2. 5: 367. 1836.

Sarothra blentinensis P. Savi, Nuov. Giorn. Pisan. 39: 225. 1839. Type: Italy, Bientina, 1936, *Savi* FI.

H. blentinense (P. Savi) Walp., Rep. 1: 384. 1842.

Sarothra mutila (L.) Y. Kimura in Nakai & Honda, Nov. Fl. Jap. No. 10: 232. 1951.

Common Name: Dwarf St. John's-wort; Small-flowered S.; Slender S. Plate 17. Map 5.

Glabrous, somewhat rhizomatous perennials, 0.5-(1.5)-2.9 dm tall, curved-ascending at the base, the stem 4-angled or 2-ridged and somewhat flattened, narrowly winged on the corners, usually once or twice branched in the upper part, sometimes simple, axillary short-fascicular branches often also present. Roots fibrous, arising from the stem base or the rhizomes. Leaves pellucid dotted, sessile and clasping, the pairs spiral but not decussate, ovate, elliptic, or oblanceolate but generally obtuse, those of secondary branches smaller and more slender that the principal ones, the median leaves 0.45-(1.0)-2.0 cm long, 0.2-(0.5)-0.9 cm wide, the lower progressively smaller, more crowded and elliptic to obovate or oblanceolate. Flowers in simple or compound cymes terminal on the branches, the central member often more shortly pedicelled, the flowers and cymes subtended by pairs of bracts, the terminal flower of the cyme 4-5 mm in diameter when fully open. Sepals 5, slightly united at the base, the free sepals ca. 3.0-3.5 mm long, 0.8-1.0 mm wide, acute to obtuse, unequal in size. Petals oblong, slightly oblique, obtuse, yellow with 2-3 veins, entire, without dots, as long as the sepals or to 1 mm shorter, soon withering and caducous. Stamens 8-9, free, varying slightly in length, the anthers yellow, less than 0.1 mm long. Pistil 2.5 mm long, sessile, ellipsoid to ovoid, 3-carpellate, unilocular with 3 intruding parietal placentae, styles 3, ca. 0.5-1.0 mm long, divergent. Capsule oblong-ovoid, 3 mm long with persistent styles. Seeds light brown, 0.5 mm long, cylindrical with rounded to pointed ends, fine striate longitudinally with a sticky but not prominent caruncle.

The problem of the relationship of *Hypericum mutilum* to *H. boreale* is an intriguing one. It is evident from a perusal of large numbers of specimens that it is very difficult if not almost impossible to separate these entities with any degree of confidence. The characters which purport to separate them, namely the leaf-like versus subulate inflorescence bracts and the shape of the sepals together with the relative length of the calyx to the ovary, are extremely variable ones subject to both genetic and ecological influence. In a very general way there is a trend to have the "boreale" group of characters in the northern portion of the total range. This is evident in Ontario, where there appears to be a vague line of separation between them.

Another point to be considered is a nomenclatural one. *H. boreale* is based on Britton's (1891), rather indifferent description, which is only marginally valid at the rank of variety under *H. canadense* (see synonymy of *H. mutilum* ssp *boreale*). This variety, which was not typified, was later transferred to species rank by Bicknell (see the following synonymy). At the time that he made the transfer he made a combination under *H. mutilum* which is invalid under Article 34, because it is a name which the author did not intend to accept but only proposed in anticipation of the possible treatment of the taxon by future authors.

The taxonomic problem is further complicated by the presence of *H. canadense*, which grows sympatrically with *H. mutilum*. There are many specimens, especially from Nova Scotia and the northern New England states, which appear to intergrade with this complex so that it becomes difficult to assign them to one or the other taxon. The description of *H. dissimulatum* was a stop-gap to take care of the situation. Bicknell (1895) wrote a long philosophical discussion on how to treat the problem. Webb (1980) viewed *H. dissimulatum* as recurrent hybrids between *H. canadense* and either *H. boreale* or *H. mutilum*.

This problem is a little beyond the scope of our treatment of the Canadian species, but in order to bring some semblance of order to it, we shall retain *H. boreale* as a subspecies of *H. mutilum* L.

This complex is particularly confusing in Nova Scotia and southeast New Brunswick, possibly due to introgression with *H. canadense*. All the species in this group, *H. canadense, H. majus, H. boreale, H. mutilum* and perhaps others, have the same chromosome number, $n = 8$. It is quite likely that the degree of genetic isolation between these apparently outcrossing plants is quite low.

Key to subspecies:

A. Ultimate bracts of the inflorescence subulate; leaves pale below, oblong to ovate, mostly 5-nerved at the base, clasping; plants usually tall and rather coarse; branches with short secondary branches; in damp fields and on gravels, usually in well-drained but still damp habitats . . . . . ssp. **mutilum**

AA. Ultimate bracts of the inflorescence for the most part foliaceous, lanceolate-elliptic; leaves green below, loosely clasping to merely tapered; plants usually shorter with well-developed secondary branching in mature plants; along wet margins of streams and in swamps . . . . . ssp. **boreale**

Hypericum mutilum L. ssp. **mutilum**. Plate 6.

H. parviflorum Willd., Sp. Pl. 3: 1456. 1803, non Salisb. 1796 nec A. St.-Hil. 1828.

H. mutilum L. var. *parviflorum* (Willd.) Fern. in Rhodora 41: 549. 1939.

We are including var. *parviflorum* in the synonym of ssp. *mutilum* provisionally. The final solution of the problem is beyond the scope of this paper.

Hypericum mutilum L. ssp. **boreale** (Britt.) J.M. Gillett in Can. J. Bot. 57: 185. 1979. Plate 7.

H. canadense L. var. *boreale* Britt. in Bull. Torrey Bot. Club 18: 365. 1891. Lectotype: *Bicknell s.n.*, Maine, York Harbour, August 1888 (NY). Chosen by Webb (1980). A neotype was originally chosen by Rodriguez-Jiménez C. (1975) but cannot be accepted because the specimen was collected several years after the variety was described.

H. mutilum L. var. *boreale* Bickn. in Bull. Torrey Bot. Club 22: 213. 1895, nom. invalid.

H. boreale (Britton) Bickn. in Bull. Torrey Bot. Club 22: 211, 213. 1895.

Sarothra borealis (Britt.) Y. Kimura, l.c. 1951.

Hypericum majus (Gray) Britt. in Mem. Torrey Bot. Cl. 5: 225. 1894.

H. canadense L. var. *majus* A. Gray, Man. ed. 5. 86. 1867. Type: Canada, Ontario, Lake Superior, *Robinson* GH.

H. mutilum var. *longifolium* R. Keller in Bull. Herb. Boiss., sér. 2. 8: 184. 1908. Type: Wisconsin, *Kumlien 113* G.

Sarothra major (Gray) Y. Kimura in Nakai & Honda, Nov. Fl. Jap. 10: 232. 1951.

Common Name: Large St. John's-wort. Plates 8, 16. Map 6.

Perennial 0.8-(2.7)-3.9 dm tall. Roots fibrous, without rhizomes or runners but occasionally with short offshoots in autumn. Stem slender, smooth, green or purplish, squarish in cross section with narrow wings, the curved ascending branches appearing mostly in the upper axils, branching below when the terminal meristem damaged. Cauline leaves 1.5-(2.4)-3.8 cm long, 0.2-(0.6)-1.2 cm wide with 3-5 veins more prominent at the base, sessile, clasping or tapered below, lanceolate (in diminutive plants sometimes linear-oblong or linear-elliptic), the apex acute to obtuse, the base rounded or subcordate, basal leaves often purple, crowded, 4-5 mm long, 2-3 mm wide, somewhat obovate and rounded. Inflorescence a simple cyme in smaller plants to a complex corymbiform inflorescence in larger, the cymes subtended by subulate bracts 3-4 mm long. Flowers variable according to position in the cyme, the central the largest. Sepals of larger flowers 5, slightly united at the base, varying in size, 2 of them usually slightly longer and wider than the others, the former 4-6 mm long, 1-1.5 mm wide at the base, lanceolate, acute, streaked with oil glands and with a visible midvein and two thinner laterals. Petals obliquely ovate to oblanceolate, about the same length as the sepals or even somewhat shorter (length a function of age), yellow or pink-tinged. Stamens few (ca. 12-15) loosely fascicled, sometimes paired; the anthers round ca. 0.25 mm in diameter. Pistil ca. 3 mm long, sessile, ovoid to ellipsoid, the 3 carpels at first distinct, later indistinct, unilocular with 3 intruding parietal placentae, styles 3, separate and spreading, ca. $^1/_6$ the length of the ovary, the stigma capitate. Capsule reddish, lanceolate, blunt with persistent styles, 4-6.5 mm long; seed cylindrical, 0.54 mm long.

This species occupies a variety of habitats such as sandy or mucky shores of lakes or streams, meadows, marshes, rock crevices, mixed woods and rotting logs. These habitats have the presence of moisture in common.

Hypericum majus is sometimes confused with *H. canadensis* on herbarium sheets. A feature that contributes to confusion is the association of small plants which grow near or about larger plants. Field observations (by J.M.G.) suggest that seed

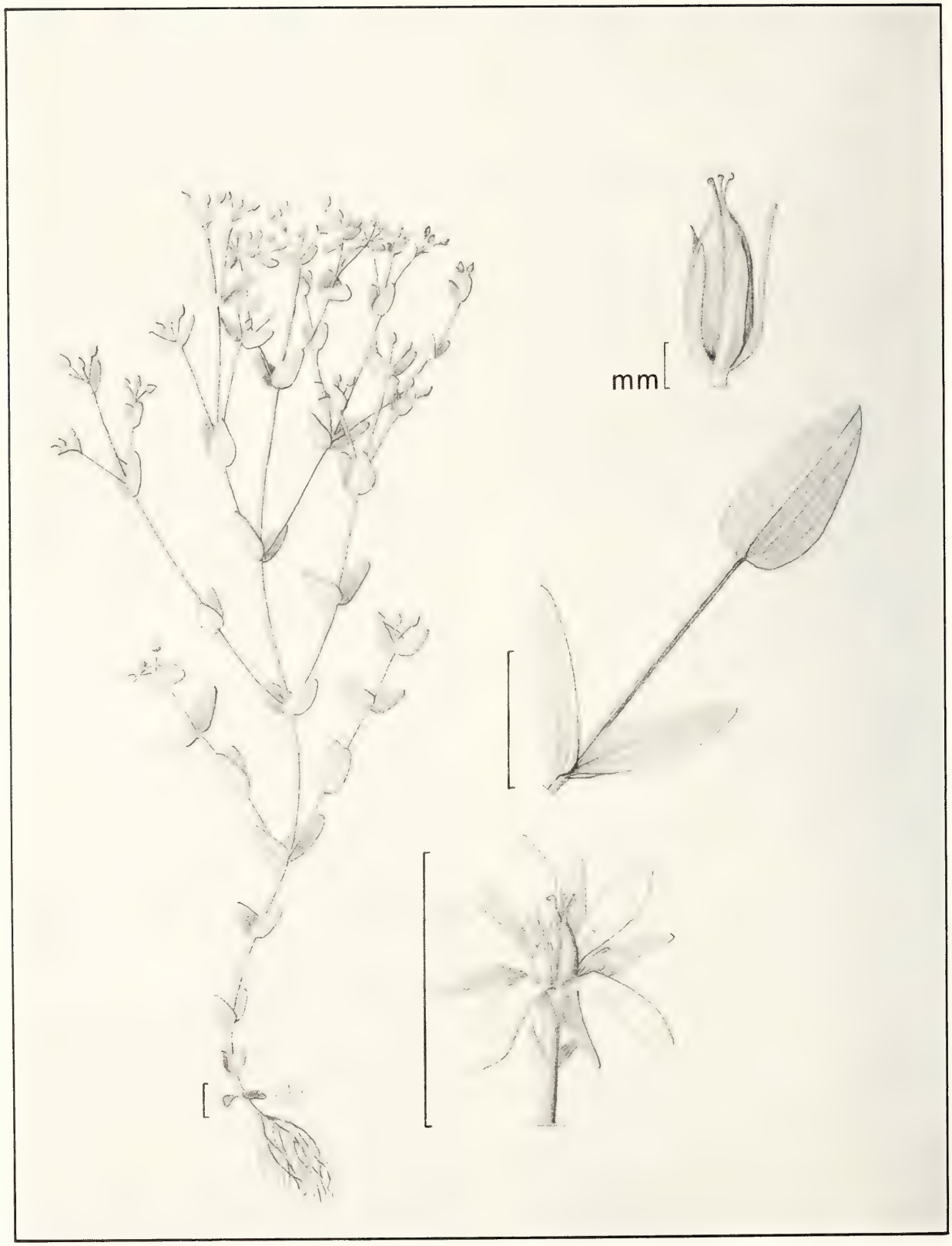


Plate 6. *Hypericum mutilum* L. ssp. *mutilum*
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

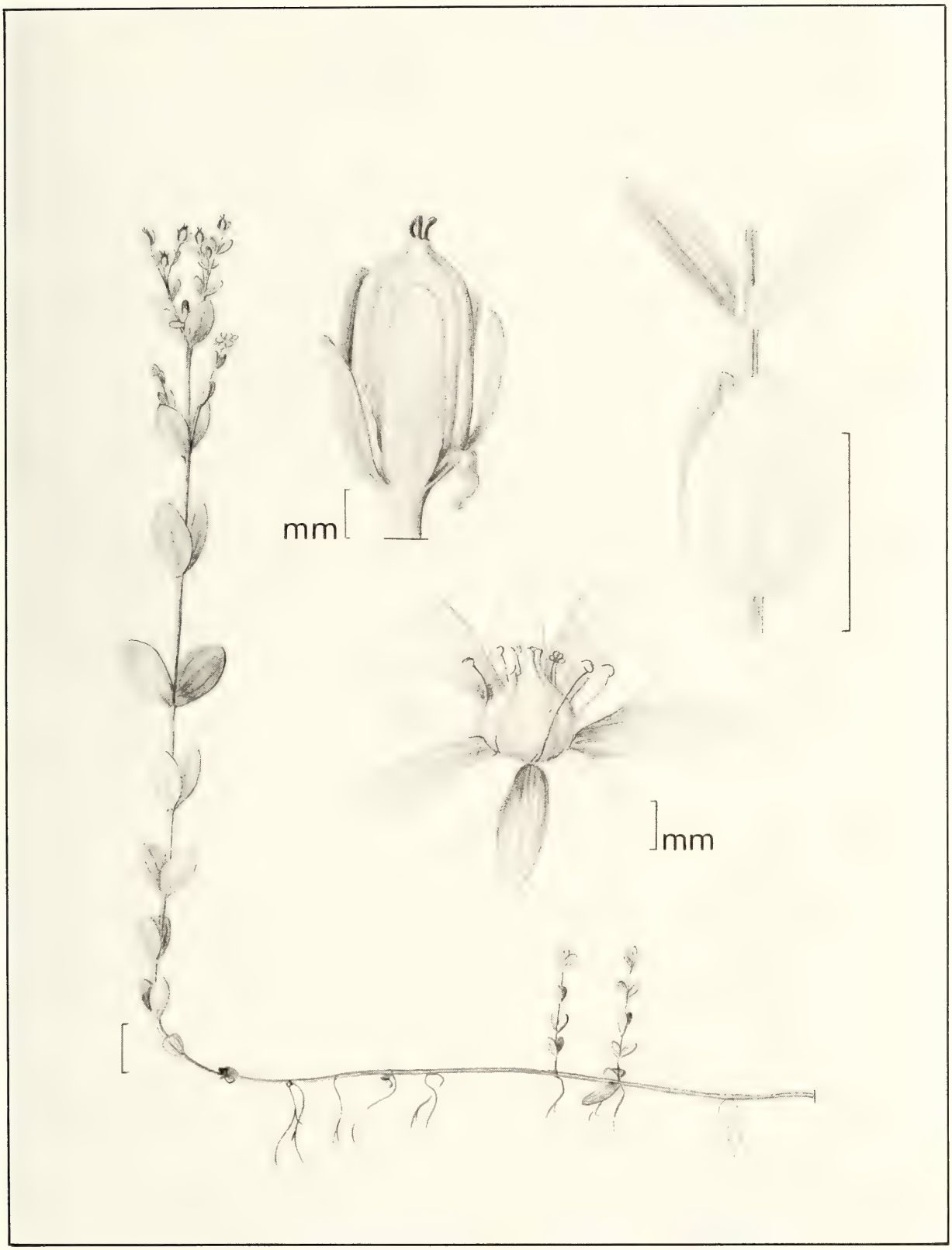


Plate 7. *Hypericum mutilum* L. ssp. *boreale* (Britton) J.M. Gillett
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

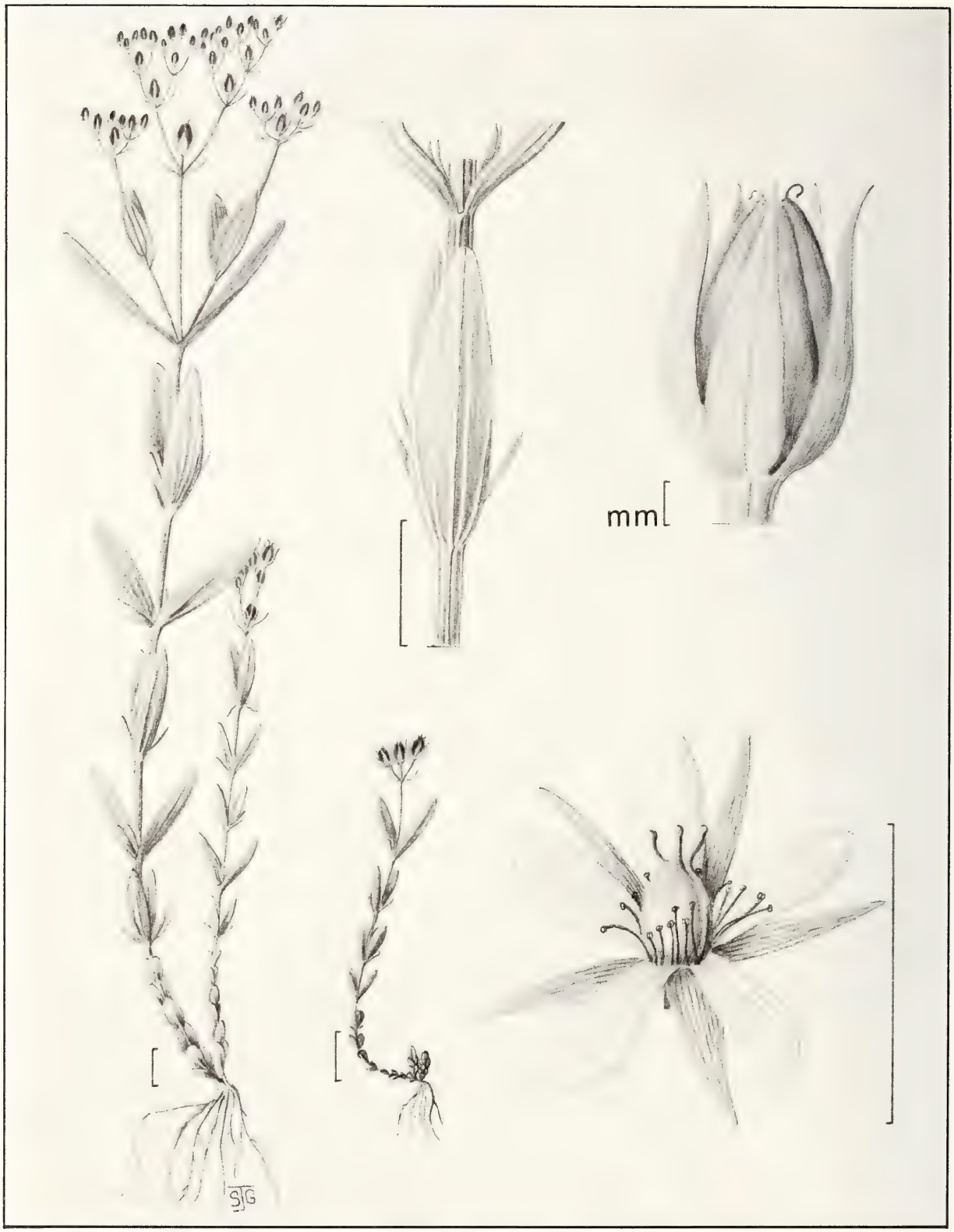
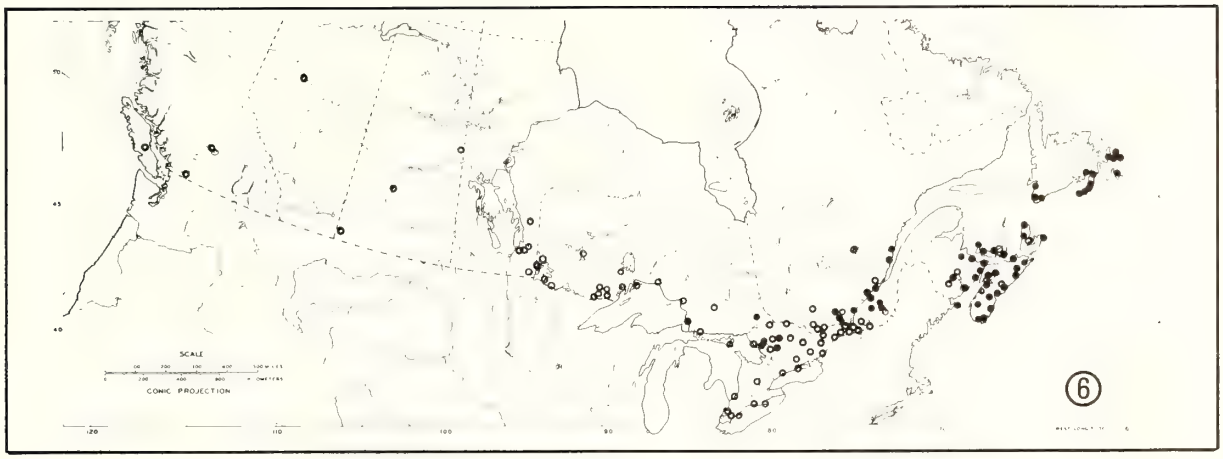


Plate 8. *Hypericum majus* (Gray) Britton
Habit of large plant; habit of small plant; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated



Map 6. Distribution of *Hypericum canadense* L. — solid dots and *H. majus* (Gray) Britton — open circles

dropped by the parent plant may germinate immediately. The young plants then may flower before they have attained full size, probably because of critical day length which has not apparently changed during their growth period. The small plants do not have morphological characteristics fully developed; thus leaves, for example, resemble those of *H. canadense*.

Hypericum canadense L. Sp. Pl. 2: 785. 1753. Type: Kalm LINN 943.26, photo DAO!

H. canadense L. [beta] *minimum* DC., Prod. 1: 550. 1824. No. 78. Canada (G-DC!) photo DAO!

H. hedyotifolium Poir., Encyc. Méth., Suppl. 3: 700, 1813. Type: [Canada?] Amer. Septent., Hb. Tournef. 2187, P!

Sarothra canadensis (L.) Rafin. in Amer. Monthly Mag. 267. 1818.

Brathys canadensis (L.) Spach. in Ann. Sci. Nat., sér. 2. 5: 367. 1836.

H. canadense L. var. *magninsulare* Weath. in Rhodora 30: 188. 1928. Type: Grand Manan, N.B., August 6, 1926. *C.A. & U.F. Weatherby 5545* GH.

H. canadense L. f. *minimum* (Choisy) Rouss. in Nat. Canad. 65: 307. 1938.

H. canadense L. var. *galiiforme* Fern. in Rhodora 49: 154. 1947. Type: Virginia, Airfield Millpond, south of Wakefield, *Fernald & Long 14962* GH.

Common Name: Canadian St. John's-wort. Plates 9, 16. Map 6.

Herbaceous, glabrous, annual, or perennial by production of basal offshoots in autumn, 3-(15)-40 cm tall, with a curved-ascending base or strict, the stem simple or branched in the upper part, 4-angled, slightly winged at the corners, rarely with short fascicular branches in the leaf axils. Roots fibrous, no rhizomes or stolons present. Leaves evenly covered with pellucid dots, sessile, tapering to the stem or subclasping, the pairs spirally arranged but not decussate, linear to linear-oblanceolate, the apex rounded, the veins 1 or 3, the 2 lateral veins weaker except near the leaf base, the median cauline leaves 7-(10.6)-16 mm long, 0.75-(1.3)-2.0 mm wide, the lower leaves often purple, progressively smaller and more elliptic, crowded by shortening of the lower internodes. Flowers solitary or in simple cymes. Branches divergent, forming an open few-flowered somewhat corymbiform inflorescence. Bracts linear-setaceous. Sepals 5, slightly united at the base, one pair slightly larger than the others, ca. 2.5 mm long (up to 4 mm long at fruiting), 0.8-1.0 mm wide, blunt-acute, longitudinally striate with 5 ridges. Petals yellow, about the same length as the sepals or shorter, oblong to oblong-lanceolate, rounded to truncate, with 5 prominent parallel veins. Stamens about 15, in 3 loose fascicles, the filaments yellow, the anthers globose, yellow, ca 0.25 mm wide. Pistil yellow, 2 mm long, ovoid, the carpels indistinct, locule 1, with 3 intruding parietal placentae, the styles 3, 0.25 mm long, (ca. $\frac{1}{3}$ the length of the ovary), separate but erect, the stigmas capitate. Capsule roseate, ovoid, 4-6 mm long, 2.0-2.5 mm wide with persistent brown styles, 0.5 mm long. Seeds cylindrical with conic to rounded ends, light brown, 0.6 mm long, longitudinally ridged with cross-pitting.

Flowering late July, fruiting from early September; both flowers and fruits occurring together.

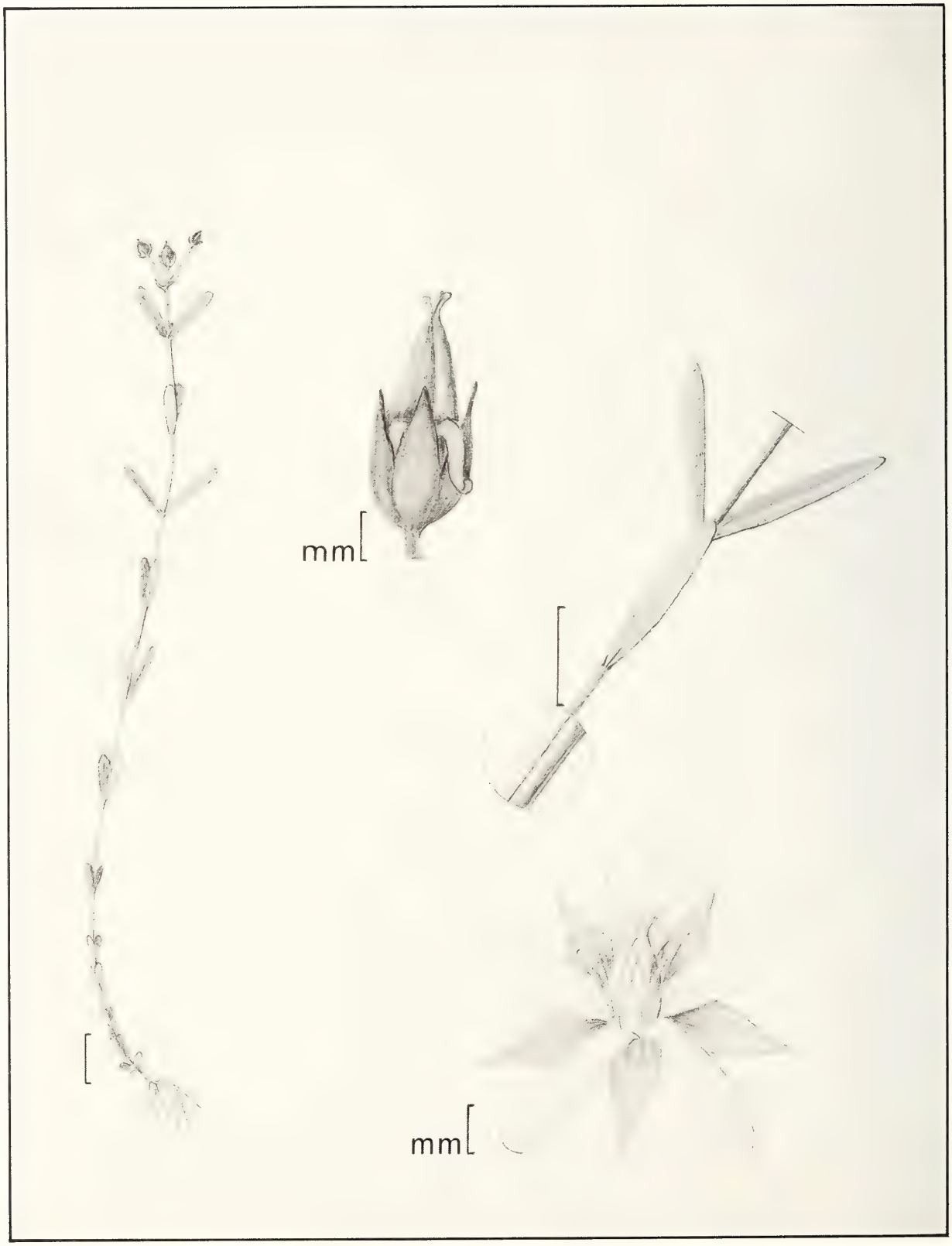


Plate 9. *Hypericum canadense* L.
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

Found in damp places, sandy ditches and clearings, roadsides, pastures, boggy or peaty areas, gravel beaches and occasionally in woods.

Geographically, *H. canadense* and *H. majus* overlap over a considerable portion of their range, *H. canadense* being primarily eastern in Canada (Maritimes) extending to Lake Superior. *H. majus* is rare in the Maritimes and extends all the way to British Columbia. In the Maritime portion of its range *H. canadense* occupies chiefly Palaeozoic formations but in Ontario it is for the most part restricted to Precambrian formations. *Hypericum majus*, on the other hand, occupies a much broader range of habitats.

In Nova Scotia, plants are found which are putative hybrids between *H. mutilum* ssp. *boreale* and *H. canadense*. These may be regarded as *H.* x *dissimulatum* Bicknell (1913) as they match material described by him from Nantucket.

Section **Roscyna** (Spach) R. Keller

Hypericum ascyron L. Sp. Pl. 2: 783. 1753.

H. bartramianum Mill., Gard. Dict. ed. 8. No. 10. 1768. Type: Cult. in Hort. Chelsea, BM!

H. pyramidatum Ait., Hort. Kew. ed. 1. 3: 103. 1789. Type: Cult. in Hort. Kew, BM!

H. ascyroides Willd., Sp. Pl. 3: 1443. 1803. Type: Pennsylvania, B.

H. macrocarpum Michx., Fl. Bor. Am. 2: 82. 1803. Type: Canada, Montreal, P.

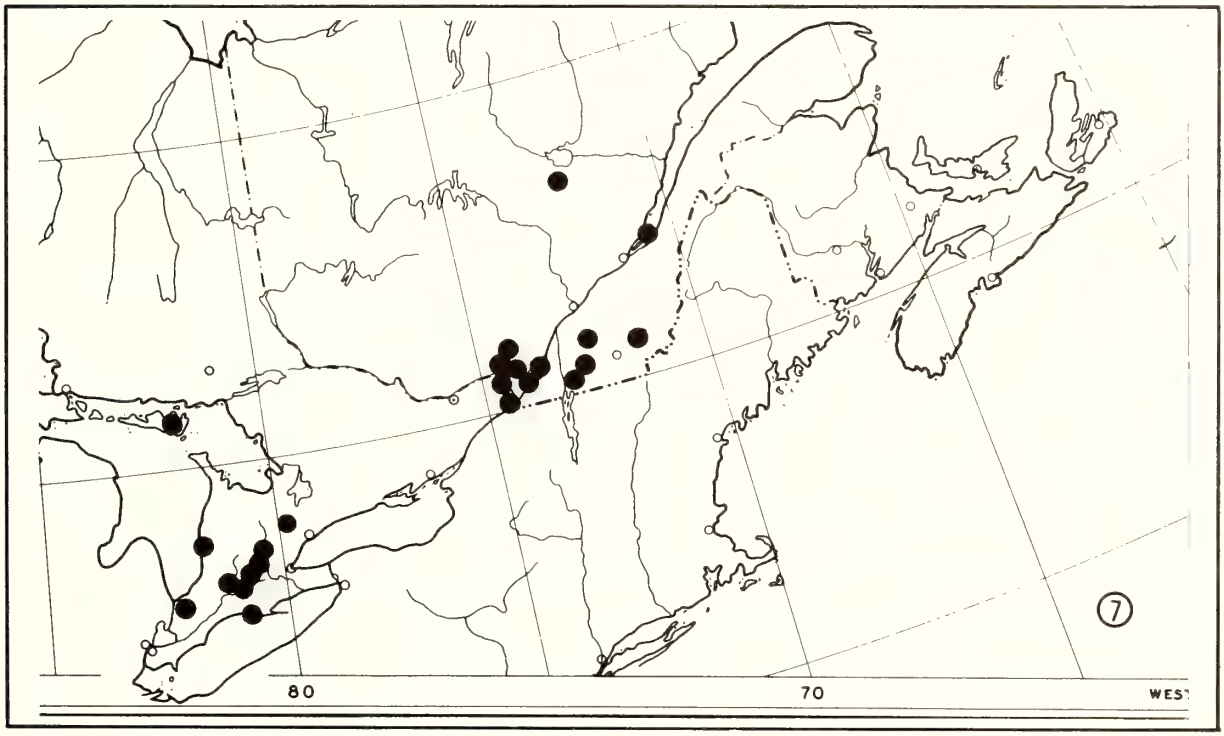
Roscyna gmelinii Spach, Hist. Nat. Vég., Phan. 5: 429. 1836.

R. americana Spach, loc. cit.

R. japonica Blume, Mus. Bot. Lugd. Bat. 2: 21. 1856.

Common Names: Great or Giant St. John's-wort; To-moe-so (Japan) Plates 10, 16. Map 7.

Stout herbaceous perennial, 0.5-2 m tall, the stem rounded below but the ascending to nearly erect branches 2-4-angled above, pith prominent. Leaves ovate-oblong, ovate-lanceolate to lanceolate, sessile and clasping, acute, pellucid-dotted, glabrous, pale below, the median leaves 4-5-(6.5)-8.0 cm long, 1.8-(2.5)-3.3 cm wide, becoming smaller towards the branch tips, midveins prominent below, the secondary pinnate veins less evident and with reticulations between them. Inflorescence a simple terminal cyme or a corymb or the flowers solitary, often subtended by the upper leaves or bracts, peduncles 1.3 cm long. Flowers yellow, showy, 5-6 cm broad, sepals 4-5, ovate, acute, ca. 1 cm long, 0.5 cm wide, deep green; petals narrowly to broadly obovate, 2.5-4.0 cm long, 1-2 cm wide, veiny without black dots. Stamens numerous (over 100), 5-adelphous, to 2 cm long, the anthers 1 mm long. Ovary 2 cm long, the styles 5, about 3-6 mm



Map 7. Distribution of *Hypericum ascyron* L.

Plate 10. *Hypericum ascyron* L.
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

long, separating and recurved slightly above, united over most of their length, the stigmas broadened. Capsule ovoid, 12-18 mm long, to 12 mm wide, dehiscing apically, the styles persistent as beaks on each segment or sometimes remaining united at the tip and separating below, the seeds brown, 1.5 mm long with a slender wing along one side.

Rich dry soil, wet roadside ditches and along streams. Flowering in mid-July; fruiting from mid-August until September.

The American plants have been considered as distinct from the Asian by many authors but, on the basis of material at hand, we feel that they are one species. The Japanese material seems to have narrower leaves than the American but material from the U.S.S.R. does not. The eastern Asian-northern American distribution pattern fits well into that discussed by Li (1952) and others. In Japan there is a long-styled variety appropriately referred to var. *longistylum* Maxim. However, considerable variation in style length occurs in the American population. It seems unwise to describe varieties based on a single characteristic, particularly when not geographically correlated.

When Aiton (1789) described *H. pyramidatum*, he was not aware of its origin. The plant was grown at the Royal Botanic Gardens, Kew. Aiton wrote that it was cultivated in 1764 by a Mr. James Gordon. However, in the second edition of the Hortus Kewensis (4: 422. 1822) he gave "native of Canada. Cult. before 1759, by Mr. Ph. Miller."

In herbarium notes, W.G. Dore has expressed the opinion that because of the sporadic distribution of the plant locally, a distribution which seems to coincide well with earlier Indian camp sites, the plant was probably distributed by the aborigines. It is not clear to what use they might put the plant. He suggests that perhaps the pods were eaten. They are at first somewhat fleshy becoming woody later.

Section **Hypericum**

Key to the species:

A. Petals black-dotted occasionally black-lined at or near the margin; capsule conic; flowers in cymes or cymose panicles

B. Styles with a distinct swelling at the base; sepals slender lanceolate, acute; punctae of the leaves round ..... **H. perforatum**

BB. Styles not swollen at the base; sepals short ovate-elliptic, obtuse; punctae of the leaves somewhat elongate ..... **H. scouleri**

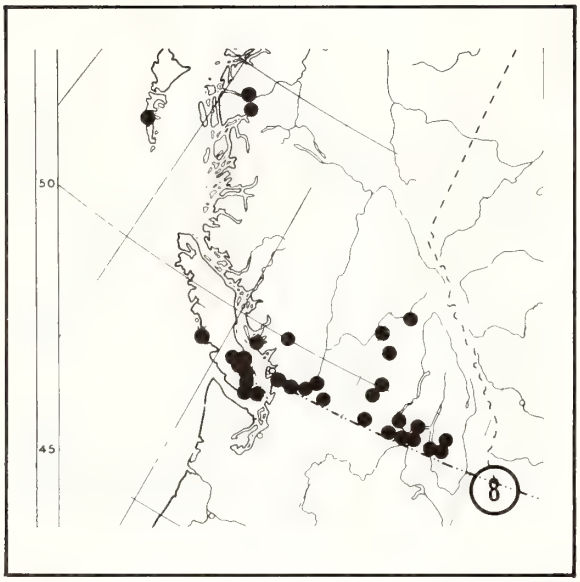
AA. Petals and sepals black-streaked throughout; capsule ovate; inflorescence corymbiform .. .. **H. punctatum**

Hypericum perforatum L., Sp. Pl. 2: 785. 1753.

(Synonyms are numerous and no attempt is made to list them here).

Common Name: Common St. John's-wort. Plates 11, 17. Map 8.

Perennial to 1 m high with 1-several erect, somewhat woody stems, profusely branched or with axillary short-fascicular branches, arising from a woody crown, the stems rusty-yellow to roseate, black-dotted or lined often with exfoliating bark at the base, 2-edged, the stems persist through the winter and the following summer, new shoots arising from the crown in autumn, these becoming the flowering stems of the subsequent year, their leaves elliptic, deep green and nearly decussate. Root slender, woody, with abundant fibrous secondary rootlets, rhizomes frequently present and giving rise to new shoots. Leaves sessile, the pairs spirally arranged but not decussate, linear, linear-elliptic, elliptic to oblanceolate, principal leaves 1.0-(1.9)-2.8 cm long, 0.31-(0.6)-1.6 cm wide, pellucid-punctate, often black-dotted, particularly at the margins, obtuse to mucronulate, entire, those of the lower part of the stem caducous, those of the axillary fascicles much more linear. Inflorescence a cymose panicle with very numerous flowers, these showy, yellow, ca. 1.5 cm in diameter. Sepals connate at the base into a firm fleshy campanulate tube, the free sepal portions slender lanceolate, pellucid, 0.3-0.5 cm long, 0.1-0.3 cm wide at the base, acute to attenuate. Petals obliquely obovate, rounded, bluntly dentate on the broadened side and purple-black punctate along the margin, the punctae sparse or absent on the straight side, about 1.5 × the length of the sepals, 0.8 cm long, 0.5 cm wide. Stamens numerous, in 3 fascicles and varying in filament length, the anthers and filaments yellow, the anthers 0.5 mm long with divergent yellow thecae, the tip of the connective purple-black. Pistil 0.3-0.5 cm long,

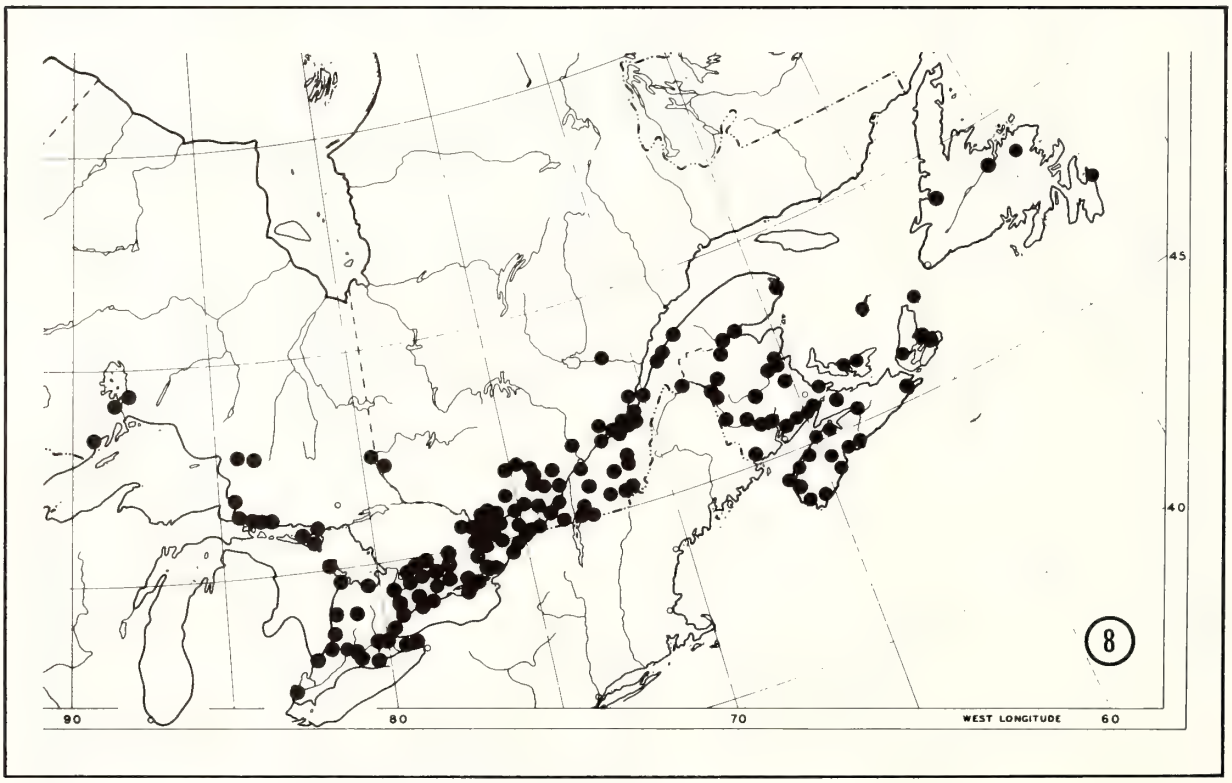


Map 8. (2 parts) Distribution of *Hypericum perforatum* L.

sessile, ovate, the 3 carpels (rarely 4) distinctly visible, the locule fully partitioned at the base, the placentation axile, becoming free central at the tip with age, the styles slightly longer than the ovary, divergent, the stigmas terminal and minutely black-punctate. Capsule apically dehiscent, the valves separating about half way towards the base. Seeds cylindrical with rounded to pointed ends, dark brown, the surface pitted, ca. 1 mm long.

Flowering takes place from June until September. St. John's-wort will invade and persist in almost any disturbed relatively dry ground whether the disturbance is due to natural causes or is man-made.

Hypericum perforatum L., St. John's-wort, Goatweed or Klamath Weed is a perennial of Eurasian origin. St. John's-wort has become a troublesome range weed in Australia, the western United States and in western Canada, particularly in British Columbia. It is also established in central Ontario and in parts of the Maritimes. Although there are other plants poisonous to cattle, Klamath Weed is the principle one. Normally livestock avoid the plant, but when forage is scarce they will graze it. The plant lowers the grazing capacity of ranges. If eaten, it causes weight loss and can be fatal. One of its toxic properties is photosensitization, which affects light-coloured skinned livestock. In order to become photosensitized the animal must ingest enough of the drug to supply the photodynamic substance. The animal then develops serious symptoms such as blistering and falling hair when exposed to strong



Map 8. (2 parts) Distribution of *Hypericum perforatum* L.

Plate 11. *Hypericum perforatum* L.
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

sunlight. These symptoms are the result of concentration of the photodynamic substances in or about nerve endings. Accompanying symptoms in cattle and sheep include high temperature, rapid pulse and respiration rates, and diarrhea. Animals having a pigmented skin are capable of screening out certain light wavelengths so that the reaction does not take place. Muenscher (1951) reported that the photosensitizing action is due to two fluorescent substances, hypericin and hypericum red. The latter may well be pseudohypericin, a closely related pigment (Watt & Breyer-Brandwijk, 1962).

St. John's-wort quickly invades disturbed land, where it displaces other cover and will invade dry areas having a non-continuous cover. Apparently it first began to become a problem in the western U.S. grazing lands about 1893 and in Canada about 1940. Attempts at first centered on chemical control, employing sodium chloride, borax, various chlorates, ammonium sulfamate and 2-4-D in various forms; but it is expensive to apply and cannot be used over large areas. Nevertheless it is still useful for small local infestations. The serious disadvantages of chemical control are the excessive cost and the leaching effect, which will damage surrounding vegetation thus contributing to the spread of the weed.

Because of these disadvantages, experimenters then turned to biological control by first studying the insect predators of *Hypericum* in native stands in Europe and then testing the various insects found to be effective. Several species of leaf-eating beetles belonging to the genus *Chrysolina* were found to be important in control. Tests indicated that the insects were adapted to different moisture zones. By the use of a moisture index it was possible to narrow the search to two or three species that would attack hypericin-bearing *Hypericum* species. For British Columbia these were chiefly *Chrysolina quadrigemina* and *C. hyperici* although a number of other species have been tested. A root-borer, *Agrilus hyperici*, has also proven to be an effective control in dry sites. The important point appears to be that the insects be introduced from a European area having similar aridity. Measurements of aridity should be made before releasing cultures; in B.C. this is roughly the area occupied by the Douglas Fir-Ponderosa Pine Association.

Actually, biological control began in Australia about 1931, where St. John's-wort was a serious pest, and in the United States about 1944, using insect material imported from Australia. The findings of the entomologists indicate that a knowledge of the ecological requirements of the insect are necessary before releasing them. When this is done, the various insects employed have been quite effective in reducing the extent of existing stands and in preventing further spread of the weed.

Hypericum scouleri Hook, Fl. Bor. Am. 1: 111. 1831. Type: *Scouler* "Northeast coast of America near the Columbia" K!

Common Name: Scouler's St. John's-wort (ssp. *scouleri*) Plates 12, 15. Map 9.

Herbaceous, glabrous, rhizomatous and often stoloniferous perennials, with 1-several stems 0.5-6 dm tall, curved ascending near the base, then erect, the stem simple or branched, slender, round in cross-section without wings, somewhat reddish brown near the base. Roots fibrous, arising from the slender woody rhizomes, these often forming a loose crown. Leaves 1.2-(1.9)-2.8 cm long, 0.6-(1.0)-1.5 cm wide, sessile, ovate to ovate-lanceolate or elliptic, clasping at the base, the lower leaves sometimes slightly petiolate, obtuse, the upper nearly acute, pellucid dotted below and purplish-black dotted along the margins, those of the smaller fascicular branches smaller and nearly linear or at least more slender than the principal cauline leaves, lower leaves early withering and caducous. Flowers 1-1.5 cm in diameter, solitary or in terminal cymes and also axillary, the pedicels 0.2-0.5 cm long, the bracts smaller than the upper leaves. Sepals 5, united about ¼ way, the free portion 3.5 mm long, 2 mm wide at the base. Petals 5, 7 mm long, 7 mm wide, yellow or somewhat roseate, purple-dotted along the margins, veiny. Stamens very numerous, 3-fasciculate, the filaments yellow, the anthers 0.6 mm in diameter and long, the thecae purple at one end. Pistil 0.5 cm long, sessile, ovoid, the carpels distinct, unilocular with 3 intruding parietal placentae, the styles 3, separated, yellow, 2 mm long with terminal stigmas. Capsule brown, ovoid, 0.7-0.8 cm long, more or less hidden by the withered petals, the 3 valves separating at the tip, the styles persistent on the segments. Seeds brown, cylindrical with rounded ends 0.75 mm long, with a longitudinally pitted surface.

Hypericum scouleri flowers from mid-June to early September with the peak around the third week of July. The higher elevation ssp. *nortoniae* flowers from late July to the end of August; fruits may be found from mid-August well into September.

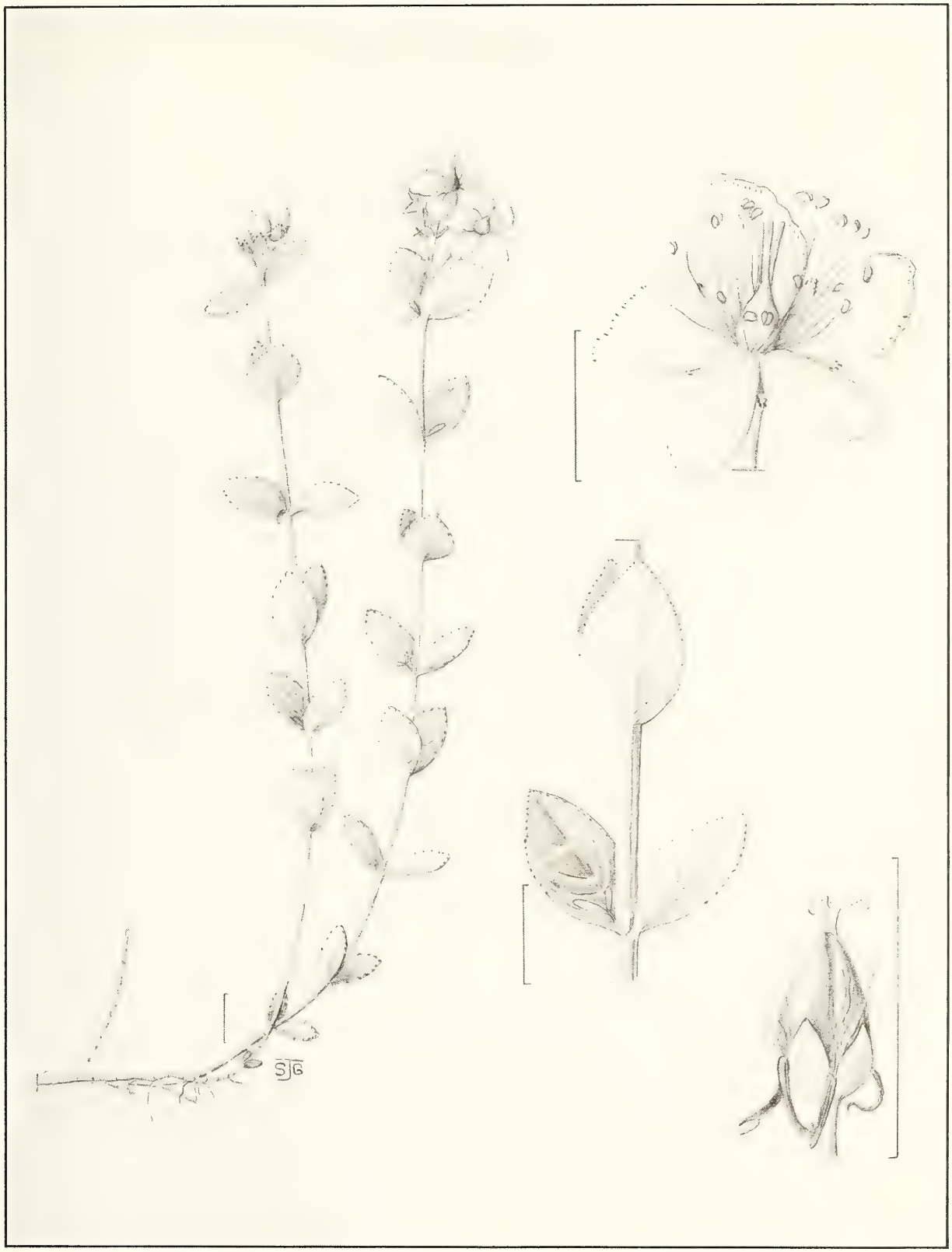


Plate 12. *Hypericum scouleri* Hook. ssp. *scouleri*
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated

Key to the subspecies:

A. Leaves slender ovate, plants 3-6 dm tall; usually branched, with terminal and axillary flowers in cymes; axillary leaf fascicles usually present ..... ssp. **scouleri**

AA. Leaves broadly ovate to elliptic; plants 0.5-2.0 dm tall, unbranched, flowers solitary or in terminal simple cymes; axillary fascicles usually absent ..... ssp. **nortoniae**

Hypericum formosum H.B.K. is a Mexican species and is related to but quite distinct from *H. scouleri* Hook. The variety *nortoniae*, which Hitchcock included in *H. formosum* subsp. *scouleri*, undoubtedly has a distinct geographical range and an altitudinal one.

Hypericum scouleri ssp. *nortoniae* is a high altitude subspecies occurring from about 1200-1500 m (4000 to 6700 ft.) on scree or gravel slopes and along wet boggy shores in fir, lodgepole pine and larch forest. Flowering is in July and August, a little later than ssp. *scouleri* which begins flowering about mid-June.

Subspecies *scouleri* is found growing in rocky open places, thickets and along shores at altitudes from near sea level to under 1200 meters.

Hypericum scouleri Hook ssp. **nortoniae** (M.E. Jones) J.M. Gillett in Can. J. Bot. 57: 185. 1979.

H. nortoniae M.E. Jones in Bull. U. Mont. Biol. 15: 39, Pl. 5. 1910. Type: *M.E. Jones*, McDonald Peak, Montana (selected by Hitchcock).

H. formosum H.B.K. var. *nortoniae* (M.E. Jones) C.L. Hitchc., Vasc. Pl. Pac. N.W. 3: 434. 1961.

Distinguished by the characteristics given in the key. The broad leaves and lack of axillary leaf fascicles are recognition features.

Hypericum scouleri Hook. ssp. *scouleri*

H. formosum H.B.K. var. *scouleri* (Hook.) Coult. Bot. Gaz. 11: 108. 1886.

H. formosum H.B.K. ssp. *scouleri* (Hook.) C.L. Hitchc., Vasc. Pl. Pacific N.-W., 3: 434. 1961; Thorne in Aliso 9: 193. 1978, superfl. comb.

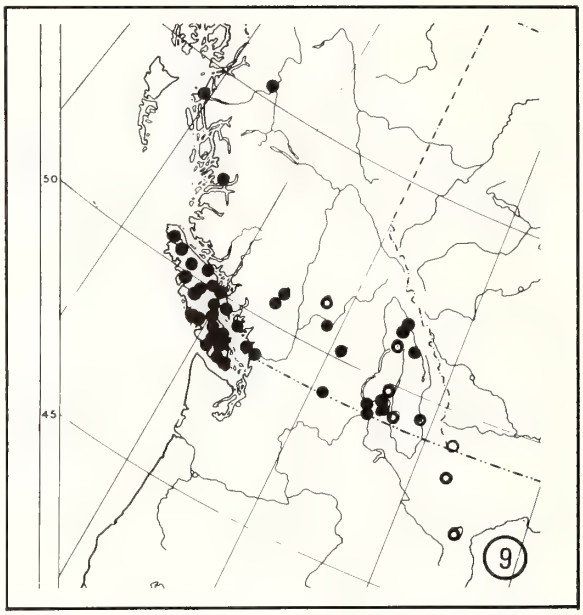
Hypericum punctatum Lam., Encycl. Méth. 4: 164. 1797.

H. maculatum Walt., Fl. Car. 189. 1788, not Crantz, 1769 nor Orsin ex Nym. 1878.

H. corymbosum Muhl. ex Willd., Sp. Pl. 3: 1457. 1802.

H. subpetiolatum Bickn. ex Small, Fl. s.e. U.S. 790. 1903.

H. punctatum Lam. f. *subpetiolatum* (Bickn. ex Small) Fern. in Rhodora 44: 429. 1942.

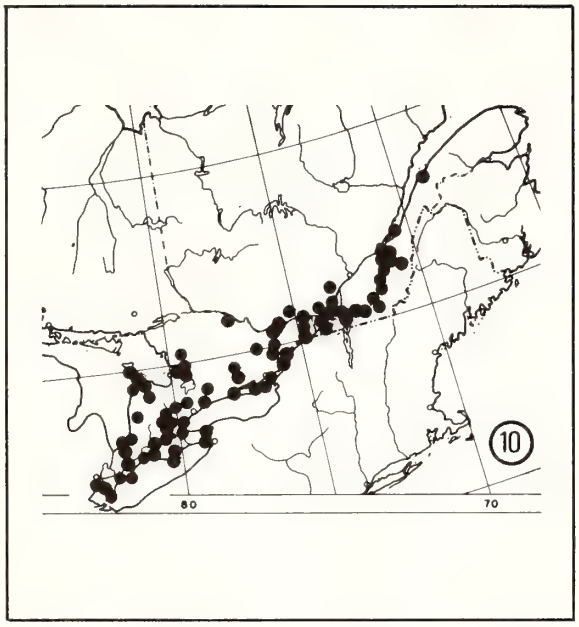


Map 9. Distribution of *Hypericum scouleri* Hook.
ssp. *scouleri* — solid dots
ssp. *nortoniae* (M.E. Jones) J.M. Gillett — open circles

Common Name: Spotted St. John's-wort. Plates 13, 17. Map 10.

Herbaceous perennial 2.5 to 9 dm high with 1-several erect, somewhat woody stems, especially woody near the base, simple or branched above, the stem terete and smooth, somewhat reddish with elongated black spots, old stems frequently persisting through the subsequent season, arising from a curved or gnarled root crown, the primary root woody, slender, secondary roots fibrous sometimes with short rhizomes. Principal cauline leaves 3.0-(4.6)-6.0 cm long, 1.0-(1.6)-2.6 cm wide, sessile or short-petioled, slightly to strongly clasping and nearly cordate, oblong-ovate, ovate or ovate-lanceolate, obtuse or slightly retuse, pellucid-black punctate, the black dots especially dense along the margins. Short fascicular branches bearing smaller oblanceolate leaves often present. Inflorescence a corymbiform cluster of compact

Plate 13. *Hypericum punctatum* Lam.
Habit; flower; fruit; portion of stem. Measurements in centimeters unless otherwise indicated



Map 10. Distribution of *Hypericum punctatum* Lam.

terminal cymes, the flowers pale yellow, ca. 1 cm in diameter, with black-streaked petals. Cymes and sometimes individual flowers subtended by linear-subulate bracts 3 mm long. Sepals 5, united at the base, the free portion lanceolate-subulate, dark-streaked, 0.1-0.3 cm long, 0.5-0.1 cm wide, acute. Petals obliquely ovate, obtuse, entire, dichotomously veined and with black streaks between the veins, ca. 0.5 cm long, 0.3 cm wide, size dependent upon age or position of cyme. Stamens numerous, in 3 loose bundles and varying in filament length, the anthers and filaments yellow (occasionally the filaments purple in late flower), the anthers ca 0.5 mm in diameter with divergent yellow thecae and purple-black connective. Pistil 0.13-0.4 cm long, sessile, ovate, 3-carpellate, 3-loculate, with axile placentation, streaked with elongate oil vescicles, styles 3, free, about half the length of the ovary, divergent, the stigmas capitate. Capsule ovate 0.5 cm long; seeds cylindrical with rounded ends, purple-brown, reticulate, ca. 0.75 mm long.

This is a species of open dry or wet woods, marshes and meadows, pastures and fields. The species has a superficial resemblance to *H. perforatum* but the distinctive corymb and heavily dotted and lined pale yellow petals readily distinguish it. Flowering takes place in late July and August; fruiting is in August and September.

Triadenum Rafin. in Medic. Reposit. N.Y. 2nd Hexadr., 5: 352. 1808, nom. nud., Fl. Tell. 3: 78. 1837, non *Triadenia* Spach (1836).

Gardenia Colden in Garden in Ess. Obs. Phys. Lit. Edinb. 2: 2. 1756. non *Gardenia* J. Ellis (1761), nom. cons.

Elodea sensu Pursh, Fl. Amer. Sept. 379. 1814, non *Elodea* Michaux, Fl. Bor.-Am. 1: 20. 1803.

Martia Sprengel, Anl. Kennt. Gewächse, ed. 2. 2: 788. 1818, nom. illegit., pro parte, quoad *H. virginicum* L.

Hypericum sect. *Elodea* Choisy, Prodr. Monogr. Hypér.: 37, 43. 1821, excl. *H. articulatum* Lam. in DC., Prodr. 1: 546. 1824.

Glabrous herbs with opposite, punctate leaves. Flowers flesh-coloured, pink to green, in terminal cymes or also axillary, occasionally solitary. Sepals 5, equal or unequal. Petals 5, somewhat oblique and unequal, imbricate in the bud. Stamens 9, united below into 3 bundles or fascicles of 3 each, these alternating with 3 conspicuous hypogynous sterile fasciclodes. Filaments rather short, attached near the center of the longitudinally dehiscent anthers. Ovary 3-carpellate, completely 3-celled. Styles free to the base, persistent on the valves of the capsule. Stigmas capitate. Capsule ovoid, apically dehiscent, septicidally. Seeds numerous, cylindrical with acute to rounded ends, the surface alveolate and without a longitudinal wing.

Type species: *T. virginicum* (L.) Rafin. based on *Hypericum virginicum* L.

Triadenum virginicum (L.) Rafin., Fl. Tell. 3: 79. 1837.

Hypericum virginicum L., Sp. Pl. ed. 2. 2: 1104. 1763. Type: Pennsylvania, *Kalm* LINN 943.27!

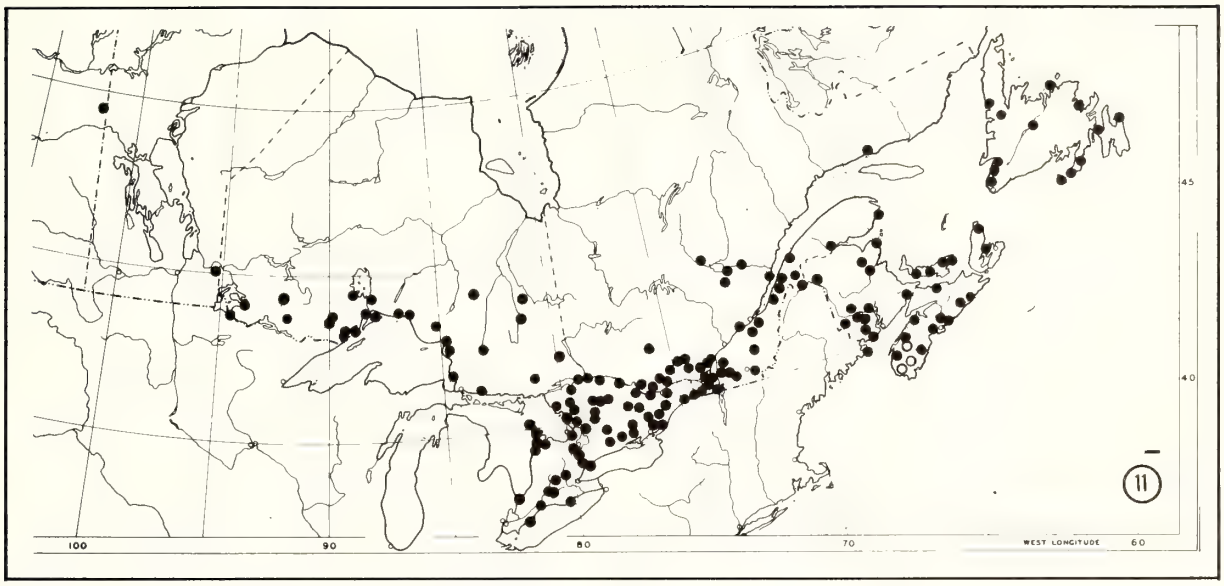
H. campanulatum Walt., Fl. Car. 191. 1788.

Elodea campanulata (Walt.) Pursh, Fl. Sept. 379. 1814.

Gardenia virginica (L.) Farwell in Am. Midl. Nat. 8: 34. 1922.

Common Name: Marsh St. John's-wort. Plates 14, 15. Map 11.

Perennial glabrous rhizomatous herbs 0.5-6.0 dm tall with 1-several erect stems, curved ascending at the base, simple or branched above occasionally with short-fascicular branches, the stems and often the whole plant green to purple, the internodes smooth, the stem rounded to somewhat angular but without wings. Rhizome merely a continuation of the aerial stem, the fibrous roots arising from the nodes. Median leaves 2.6-(3.93)-5.8 cm long, 1.5-(2.21)-3.3 cm wide, cordate or occasionally



Map 11. Distribution of *Triadenum virginicum* (L.) Raf.
ssp. *virginicum* — open circles
ssp. *fraseri* (Spach) J.M. Gillett — solid dots

rounded, ovate, elliptic, elliptic-oblong to lanceolate, obtuse to retuse, entire, dark green above, paler and often deeply purpled below, with a strong midvein and several alternate lateral veins with reticulations between them, the lower leaves gradually smaller and sometimes caducous. Inflorescence a simple or corymbiform terminal cyme with or without axillary cymes or flowers below, the lowermost subtending bracts foliaceous, those of upper cymes and flowers often subulate or nearly so. Flowers 5-merous, rather inconspicuous (opening for only a brief period of the day), flesh-coloured to pink or roseate. Sepals 4-5 mm long, 1.5-2.0 mm wide at the base, oblong-lanceolate, obtuse to acute, the veins somewhat obscured by longitudinal oil vesicles. Petals 5-7 mm long, 1.5 mm wide, oblong-elliptic, obtuse with 5 whitish veins from the base. Stamens 9 in 3 bundles of 3, the latter united about $^1/_3$ of their length and one episepalous, alternating with 3 yellow sterile fasciclodes 1.5 mm long; anthers less than 0.5 mm long, soon caducous. Pistil 4 mm long, ovoid, styles 3, 1.5 mm long, stigmas capitate, the carpels visible, locule 1, with 3 intruding parietal placentae. Capsule deep maroon, to 1.2 cm long, the valves separating partly their whole length along the carpel sutures but dehiscence terminal, the styles persistent. Seeds 0.5 mm long, cylindrical with apiculate rounded ends and sticky pitted surface, light brown. Flowering in early August; fruiting from late August until October. n = 19

Key to the subspecies:

A. Sepals lanceolate, acute to acuminate, to 7 mm long; styles 2-3 mm long ..... subsp. **virginicum**

AA. Sepals elliptic to ovate, obtuse, 2.5-5.0 mm long; styles 0.5-1.0 mm long .... subsp. **fraseri**

Triadenum virginicum (L.) Rafin. ssp. **virginicum**

This subspecies is chiefly a coastal plain element but also occurs south of the Great Lakes in New York, Ohio, Indiana, Illinois and Wisconsin. A few specimens having a scattered distribution come from Nova Scotia. We have an interesting specimen or rather doubtful quality from Go Home, Muskoka District, Ontario, collected by A.G. Huntsman, July 29, 1904 (CAN).

Triadenum virginicum (L.) Rafin. ssp. **fraseri** (Spach) J.M. Gillett, Can. J. Bot. 57: 186. 1979. *Elodea fraseri* Spach in Ann. Sci. Nat., sér. 2. 5: 168. Lectotype: Canada, *Fraser* (FI).

Plate 14. *Triadenum virginicum* (L.) Raf. ssp. *fraseri* (Spach) J.M. Gillett
Habit; flower; fruit; portion of stem. Measurement in centimeters unless otherwise indicated

Hypericum virginicum var. *fraseri* (Spach) Fern. in Rhodora 38: 434. 1936.

Triadenum fraseri (Spach) Gleason in Phytologia 2: 289. 1947.

This is our most abundant taxon and extends from Nova Scotia to Saskatchewan. Boivin (1967) reported it as an introduction in peat brought to British Columbia from the east of the country.

Acknowledgements

We should like to acknowledge the contribution of Dr. Peter Harris, Canada Agriculture, Research Branch, Regina, Saskatchewan for data and reprints relevant to the biological control problem. Gerald Fitzgerald of the Palaeobiology Division, National Museum of Natural Sciences, assisted in seed photography. The drawings are by Sally Gadd.

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Plate 15. Seed. Figs. 1, 2 *Hypericum ellipticum*; figs. 3, 4 *Triadenum virginicum*; figs. 5, 6 *Hypericum anagalloides*; figs. 7, 8 *H. scouleri* ssp. *scouleri*. Scale: White bar = 0.5 mm. Black bar = 1.0 mm

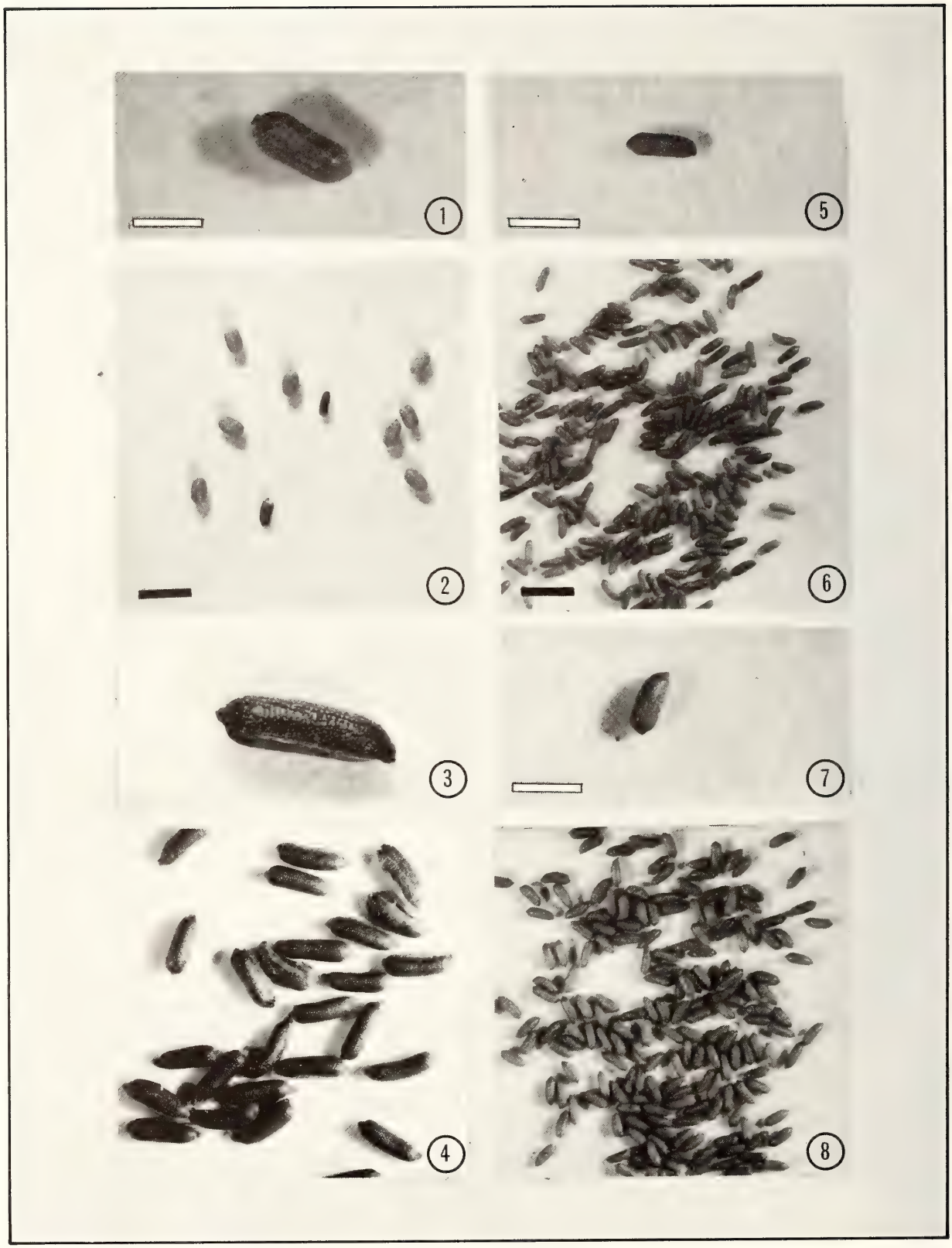

Plate 16. Seed. Figs. 1, 2 *Hypericum gentianoides*; figs. 3, 4 *H. ascyron*; figs. 5, 6 *H. majus*; figs. 7, 8 *H. canadense*. Scale: White bar = 0.5 mm; Black bar = 1.0 mm

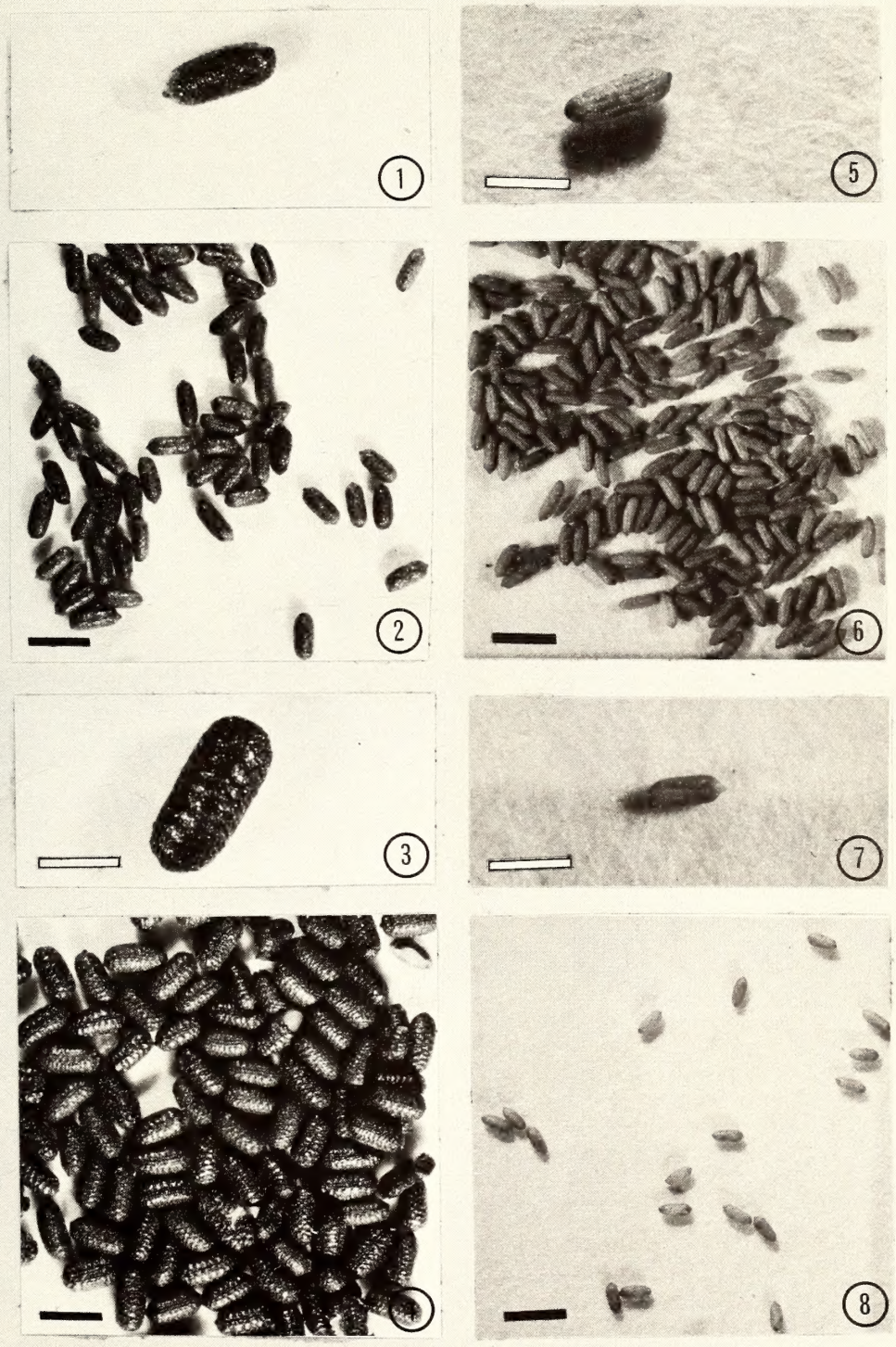

Plate 17. Seed. Figs. 1, 2 *Hypericum punctatum*; figs. 3, 4 *H. perforatum*; figs. 5, 6 *H. mutilum* ssp. *boreale*; 7, 8 *H. mutilum* ssp. *mutilum*; Scale: White bar = 0.5 mm; Black bar = 1.0 mm

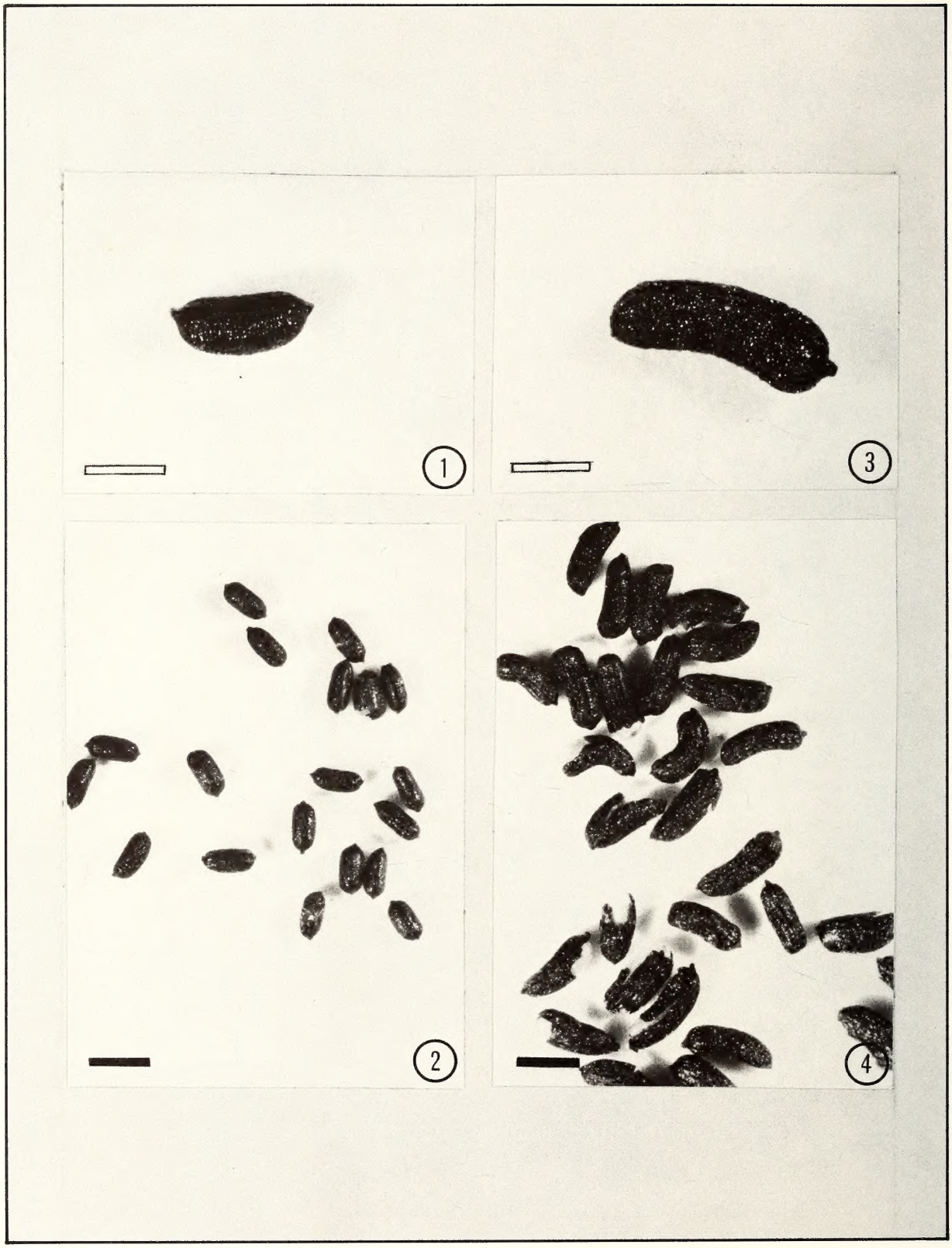

Plate 18. Seed. Figs. 1, 2 *Hypericum kalmianum*; figs. 3, 4 *H. prolificum*. Scale: White bar = 0.5 mm; Black bar = 1.0 mm

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